EFFECT OF EARTHQUAKE AND STORM DISTURBANCES ON BULL KELP (*DURVILLAEA* SPP.) AND ANALYSES OF HOLDFAST INVERTEBRATE COMMUNITIES

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in Environmental Sciences at the School of Biological Sciences, University of Canterbury, New Zealand

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Dedicated to my dad Giorgio.

Abstract

Marine wave-exposed intertidal rocky shores, in the temperate zone, are some of the most productive yet highly stressful biological habitats on earth. In the intertidal zone, marine species experience daily changes in desiccation, temperature and light conditions. Many large canopy-forming seaweeds, including some laminarian kelps and many fucoids, are well-adapted to these conditions, but are typically being limited in their upward distribution on the shore by desiccation tolerances. These rocky shores are also characterized by physical and biological disturbances, such as storm waves, invasions by non-native species and even tectonic events like vertical displacement following earthquakes. Where kelps and large fucoids dominate the biomass, they control and modify ecosystem functions, like productivity, wave attenuation and light levels. Southern bull kelps (*Durvillaea* spp.), which are actually fucoids, are some of the largest marine habitat formers on earth, often dominating wave exposed intertidal and shallow reefs throughout much of temperate Australasia and South America. Bull kelps support high local primary productivity, attenuate waves and provide food for grazing fish and habitat for invertebrates. A bull kelp is composed of a large holdfast firmly attached to the rocky substratum, a stipe and a flexible buoyant frond. Bull kelp can grow up to 10 m and live up to 10 years. Only a few species live on the stipe and fronds of bull kelp but their large holdfast can provide habitat for many invertebrates. In this thesis I explore, from intertidal reefs along the east coast of the South Island of New Zealand, how bull kelp (*Durvillaea poha* and *D. antarctica*) respond to simulated storm disturbances (Chapter 2), how their holdfast provide habitat for invertebrates (Chapter 3), and I describe impacts on bull kelp following a large earthquake and uplift of coastal reefs (Chapter 4).

Firstly, I compared bull kelp responses between undisturbed control plots and three simulated disturbance intensities. To simulate a typical gradient in storm-disturbance effects, I removed either holdfasts, stipes or blades at two reefs at Moeraki and one reef at Oaro. Four months after these disturbances, there were no major effects on density or sizes of adult holdfasts in the stipe removal treatments, demonstrating that after growth has ceased these biological structures can remain intact and attached to the rocky substratum. I found no disturbance-driven effects on either the density or the length of juvenile blades. Overall, juvenile densities were highly variable in space and time. I also found that, at the two Moeraki reefs, the length of juvenile bull kelp show strong increases in all treatments. In addition, most bull kelp with blades showed sign of recovery, with new growing tips along the margins of cut tissue. Finally, all disturbed plots were rapidly colonized by fast growing opportunistic seaweeds, as the green

alga *Ulva* spp. colonized disturbed reefs at Oaro and the invasive kelp *Undaria pinnatifida* colonized disturbed plots at Moeraki. I also found a negative correlation between the abundance of these early colonizers and the density of bull kelp recruits, indicating either that the former inhibits new bull kelp recruitment, or that small bull kelp recruits can inhibit colonization of opportunistic seaweed.

Secondly, I collected *Durvillaea poha* holdfasts to test if holdfast-associated invertebrates differ between different sites located along a latitudinal gradient in the South Island of New Zealand and between different holdfast sizes. The result from these collections showed higher biodiversity at the mid-latitudinal reefs, but this could probably be explained by low and high latitudinal holdfasts being either stressed by uplift or by a few size-outliers, respectively. I also found, as in past kelp holdfast studies, strong size-abundance relationship, that is, larger holdfasts were inhabited by more invertebrates than small holdfasts. I then tested, in a factorial short-term transplant experiment, if colonizing invertebrates differed between different holdfast morphologies (round vs. elongated), holdfast types (live vs. 3D printed abiotic models) and holdfast species (*Durvillaea poha* vs. the early colonizing non-native *Undaria pinnatifida*). I found, for similar sized holdfasts, that more invertebrates were associated with live than abiotic holdfasts and with *Undaria* compared to *Durvillaea* (but with no effects of holdfast shape). These results suggest that invertebrates may partially consume holdfasts and use small interstitial spaces associated with complex biological structures. Although *Undaria,* for similar sized holdfasts, supported more invertebrates than bull kelp the *Undaria* habitat is, however, more ephemeral because this holdfast persists for less than one year compared to up to 10 years for bull kelp.

Finally, I surveyed 16 reefs from Oaro to Kaikōura peninsula 3-4 months after a 7.8 M_w earthquake with an epicentre located 4 km from the rural village of Waiau. Of these reefs Oaro experienced 0.2 m submergence, whereas the remaining reefs were uplifted from 0.4 to 2.2 m. At each reef, 50 × 50 cm quadrats were sampled, by taking photos perpendicular to the substratum, in the zone that, prior to the earthquake, was dominated by bull kelp. This zone was subdivided into a higher zone turned white due to decaying calcifying encrusting organisms, a middle zone turned green due to colonization of the opportunistic *Ulva* spp seaweed, and a lower red zone where the red encrusting understory alga remained relatively intact. In total, 1658 quadrats were analysed for (a) percent cover and (b) density of 'holdfast scars' (circular areas of newly exposed fresh rock), (c) stipes without blades, (d) stipes with blades, and (e) percent cover of holdfasts. I found for the 15 uplifted reefs that cover and

number of holdfasts scars were greatest in the white zone, that densities of stipes with blades and cover of attached holdfasts were highest in the red zone, and that densities of stipes without blades were highest in the mid-green zone. By contrast, there was no white zone at the single reef experiencing slight submergence (Oaro) and this reef had fewer holdfast scars and stipes without blades. I also tagged stipes from the green zone from 9 uplifted reefs as well as stipes from Oaro. Ca. 8 months later all tags were lost from the bull kelp from the uplifted reefs but all tags survived at Oaro, suggesting that most kelp in the green uplifted zone would eventually die.

Overall, my study documented that bull kelp are resilient to small scale storm-disturbances as they can recover from pruned blades or through formation of a new canopy from rapid growth of understory juveniles. I also found that when perennial kelps were lost they were replaced by opportunistic seaweeds, both following small-scale manipulated and large-scale uplift-related disturbances. Importantly, when bull kelp and their holdfasts are lost, so is the rich fauna that inhabits these biological structures. Finally, I documented extensive loss of bull kelp following an earthquake, a result that likely can be extrapolated to other areas of the coastline that experienced similar or more severe uplifts. These large-scale losses are likely to have long-lasting and wide-ranging ecological effects and it will be of great interest to study these seaweeds beds in the future, to test if these past extensive bull kelp assemblages will recover fully or if remnant surviving beds will remain small.

Chapter 1: Introduction

1.1 Habitat of large canopy-forming seaweed

Marine wave-exposed intertidal rocky shores are some of the most stressful biological habitats on earth (Stephenson and Stephenson 1949, Raffaelli and Hawkins 2012). In this zone, large canopy-forming seaweeds experience daily changes in desiccation, temperature, light and wave battering. In addition, natural disturbances and stressors cause die-off of canopy forming kelps and fucoids, for example through herbivory, competition, diseases, storms and even coastal uplifts (Castilla 1988, Castilla and Oliva 1990, Benedetti-Cecchi et al. 2001, Steneck et al. 2002, Connell et al. 2008). These algal habitats support a diverse group of benthic invertebrates and fish, typically dominated by crustaceans, molluscs and polychaetes (Cancino and Santelices 1980, Dayton 1985, Smith and Bayliss-Smith 1998, Bruno and Bertness 2001, Taylor and Schiel 2005, 2010). Interactions between the large seaweeds, that provide physical structure and ecological functions to smaller organisms, have been studied in detail. Typically, these ecologically important species are referred to as foundation species, habitat formers, ecosystem engineers, keystone structures or structural species (Dayton 1972, Huston 1979, Jones et al. 1994, Tews et al. 2004, Schiel 2006, Thomsen et al. 2010, Angelini et al. 2011). For example, forests, coral reefs, mangroves, seagrass, oysters and kelp forests all provide shelter from predators, food for consumers, and reduce stressful environmental conditions (Stachowicz 2001, Bruno et al. 2003). On lower intertidal rocky shores, canopy forming seaweeds like the kelps *Laminaria*, *Hedophyllum* and *Lessonia* and the fucoid *Durvillaea*, represent habitat forming foundation species (Smith and Bayliss-Smith 1998, Schiel and Hickford 2001, Schiel and Foster 2006, Schiel and Lilley 2011, Smale et al. 2013, Smale and Wernberg 2013, Steneck and Johnson 2014, Schiel and Foster 2015, Teagle et al. 2017). Canopies of kelps and fucoids are particularly important in transforming the harsh intertidal habitat into a suitable shelter for invertebrates and they represent an important source of food for grazers, like the butterfish *Odax pullus* (Dayton 1985, Smith and Bayliss-Smith 1998, Bruno and Bertness 2001, Taylor and Schiel 2005, 2010). In addition, kelps and fucoids can also inhibit turf forming algae by whiplash effects from their large fronds, and control nutrients availability and light regimes (Bruno and Bertness 2001, Kendrick et al. 2004, Taylor and Schiel 2005, Wernberg et al. 2005, Wernberg and Connell 2008, Connell and Russell 2010). Thus, large perennial canopy forming kelps and fucoids create habitats that increase biodiversity and productivity of coastal areas.

1.2 Bull kelp

First described by Bory de Saint-Vincent (1826) *Durvillaea* is a genus of brown algae in the Order Fucales (class Phaeophyceae). These large canopy-forming fucoids colonise and dominate many intertidal and subtidal fringes of cold-water wave exposed rocky shores of the southern hemisphere. *Durvillaea* species are found from 45° to 60° S in Chile, New Zealand, Australia, Tasmania and the sub-antarctic islands (South and Hay 1979, Smith and Bayliss-Smith 1998, Taylor and Schiel 2005). The extensive morphological plasticity of this genus has caused confusion over the different recognised species, and species numbers vary from 4 to 7 depending on authorities (Hay 1977, 1979, Fraser et al. 2009, Fraser et al. 2012, Weber et al. 2017). Two additional issues complicate the nomenclature of '*Durvillaea* bull kelp'. First, bull kelp is also the common name used for *Nereocystis luetkeana*, a true kelp in the Order Laminariales, which dominate along northeast Pacific coastlines. Second, bull kelp is not a true kelp, as this term normally is used only for seaweed within the Order Laminariales (Schiel and Foster 2006). *Durvillaea* species differ from true kelp by having simple direct life histories (Fig. 1.1). Gametes are mainly produced in winter in conceptacles on separate male and female plants. Eggs and sperm are released into the water column where they fertilize. A large individual can produce millions of eggs. Most fertilized eggs settle within a few meters from parent plants (Hay 1977, Santelices et al. 1980, Westermeier et al. 1994, Taylor and Schiel 2005, Schiel et al. 2006, Tala et al. 2013), although dispersal from drifting adults can cover large distances (Fraser et al. 2011).

Durvillaea species have many similar ecological, morphological and functional traits as true kelps and are therefore often included with these in reviews of kelp ecology (Steneck et al. 2002, Teagle et al. 2017). In this thesis, I studied the ecology of two intertidal *Durvillaea* species: *D. antarctica* and *D. poha*, also referred to as 'southern bull kelp'. These two species have a large blade that can reach 10 m in length, live for up to 10 years, and provide standing biomass of up to 80 kg/m^2 (Schiel 1990, Steneck et al. 2002, Taylor and Schiel 2005, Schiel and Foster 2015). Each *Durvillaea* individual is composed of a holdfast, a stipe and a blade (frond, lamina, i.e., the main photosynthetic area of the plant) (Fig. 1.2). The typically dome-shaped discoid or oval holdfast has a strong attachment to rocky substratum, where large individuals require forces in excess of 1000 Newton to be dislodged (Smith and Bayliss-Smith 1998, Thomsen and Wernberg 2005). Holdfasts positioned close to each other can coalescence during growth to form a single large holdfast with multiple stipes and blades, where each stipe-blade represents a unique genotypic individual (Hay 1977). Adult holdfasts often have many

holes and cavities excavated by grazing invertebrates, and these holdfast attributes are rarely present in the congeneric species *D. willana*, that typically occur below D. antarctica and D. poha in the adjacent shallow subtidal zone (Hay 1977). A cylindrical non-branched stipe links the holdfast to the blade (by contrast, *D. willana* has branched stipes) (Fig. 1.2). The blade is composed of a central medulla, covered by a meristoderm, where cell division occurs during growth, and an outer cortex layer. The main meristem is located just above the stipe, so damage below this growth centre is likely to cause mortality (Roberts 1979). The medulla is characterized by a honeycombed cell structure so that the blade is positively buoyant (Hay 1977) and dislodged bull kelp can persist for long times and drift long distances (Smith 2002, Collins et al. 2010, Fraser et al. 2011, Tala et al. 2013, Cumming et al. 2014). Colour and shape of the blade can change within and between species and with ambient environmental conditions and are therefore not entirely useful traits to identify species. *D. antarctica* and *D. poha* were long described as a single species (*D. antarctica*) where morphological variations were attributed to plastic adaptations to different shore topographies and wave action (Hay 1977, South and Hay 1979, Fraser et al. 2009, Fraser et al. 2012). More specifically, *D. antarctica* blades are typically characterized by slim long 'thongs', a low drag morphology that is better adapted to breaking waves. This morphology was traditionally referred to simply as 'thonged' or 'high impact' morphologies, whereas the wider and less branched blades of *D. poha* were defined as the 'cape' morphology (Fig. 1.2A and 1.2B) (Hay 1977, South and Hay 1979, Fraser et al. 2009, Fraser et al. 2012). In addition to this key difference in blade morphology, Hay (1977) noted different stipe lengths and holdfast sizes being shorter and smaller in the 'cape' form, and in the frond honeycomb structure that is fully extended and thicker on the entire frond of the 'thonged' form. However, recent genetic studies have demonstrated that the two morphologies have different genotypes that represents two separate species, of which *D. poha* is endemic to New Zealand (Fraser et al. 2009, Fraser et al. 2012). These two species can form extensive canopies that can erode the rocky substratum when holdfasts and underlying rocks break off during storms (Smith and Bayliss-Smith 1998).

1.3 The Kaikōura earthquake

Located at the edge of the Australian and Pacific plates, and primarily involving the Marlborough Fault System, the Kaikōura earthquake has been described as one of the most complicated ruptures ever recorded (Clark et al. 2017, Hamling et al. 2017). On the 14th November 2016, at 12.03 a.m., a 7.8 M_w (magnitude moment) multi-fault earthquake struck

north the Canterbury region, with the epicentre located 60 km south-west of the tourist town of Kaikōura and 4 km from the rural town of Waiau (Clark et al. 2017, Hamling et al. 2017, Kaiser et al. 2017) (Fig. 1.3). With a shallow hypocentre of 15 km, and involving both major and minor inshore and offshore faults, slips, and vertical displacements, this earthquake impacted the Kaikōura region along ca. 130 km coastline from Oaro to Cape Campbell (Fig. 1.4). The high variability in fault deformations is evident from the different levels of vertical uplift along the coastline, from 0.4 to 4.8 m (± 0.5) (Clark et al. 2017, Hamling et al. 2017). Ecological impacts of seismic uplifts on rocky shore benthic organisms have been reported from Alaska, Japan and Chile, where widespread damages were documented on many intertidal species (Haven 1964, Bodin and Klinger 1986, Castilla and Oliva 1990, Castilla et al. 2010, Noda et al. 2016), including high mortality of intertidal canopy forming seaweed. It is therefore likely that the Kaikōura earthquake have caused similar high mortality with potentially large and wide ranging ecological consequences.

1.4 Study sites

Fieldwork was conducted on the east coast of the South Island of New Zealand at the Kaikōura Peninsula (42°25’29’’S 173°43’03’’E), Oaro (42°30’59’’S 173°30’22’’E), Pile Bay, on Banks Peninsula near Christchurch (43°37’05’’S 172°45’52’’E), and Moeraki, just north of Dunedin (45°21’54’’S 170°51’48’’E), that is, along a latitudinal gradient from 42 to 45 degrees, representing both healthy and uplifted reefs (Fig. 1.4). Eastern New Zealand rocky coastlines are usually dominated by sedimentary relatively-soft rocks, as seen at study sites at Kaikōura, Oaro and Moeraki. However Pile Bay, located on Banks Peninsula, is composed of harder volcanic and metamorphic rocks (Schiel 2004). Water circulation patterns in this area are dominated by cold sub-antarctic waters, carried by the Southern Current and warmer coastal waters (Schiel 2004). On average, these sites have an annual sea surface temperature of ~12 °C, that is subjected to seasonal variations of up to 10 °C and are further influenced by the El Nino Southern Oscillation (Greig et al. 1988). Canopy forming seaweeds can be relatively sensitive to climatic variations in these regions (Schiel et al. 2016), in particular, air temperature and the Southern Oscillation Index (but also variations in sea surface temperatures and wave height) (Schiel et al. 2016).

1.5 Study aims

This study is divided into three data chapters, each addressing research related to the ecology of bull kelp in New Zealand. More specifically, my aims are to quantify (a) recovery processes following natural storm-associated disturbances, (b) which holdfast attributes control associated invertebrate communities and (c) bull kelp losses following the Kaikōura earthquake and associated reef uplifts.

In Chapter 2, I test the hypothesis that more disturbed plots have less bull kelp recovery. This hypothesis was tested on reefs at Oaro and Moeraki, where I quantified how recruits and adult bull kelp responded to having blades, stipes or holdfasts removed. In this chapter I also quantified how disturbed plots got colonized by fast-growing opportunistic seaweed.

In Chapter 3, I test the hypothesis that holdfast-associated invertebrates vary between reefs from different latitudes and increases with holdfasts sizes, by collecting holdfasts from the four main study regions. I also addressed the hypothesis that holdfast type (live or plastic mimics), shape (oval or round) and kelp species (comparing results to holdfast of the invasive kelp *Undaria pinnatifida*) affect colonization of mobile invertebrates.

Finally, in Chapter 4, I describe impacts on bull kelp following a large earthquake and uplift at 15 reefs along the Kaikōura coastline. The aim here was to provide baseline data on kelp losses after an extreme and rare large-scale disturbance event. Such baseline data are important to understand the future ecology of this coastline, as well as how large-scale disturbances may have long-lasting impacts that cannot be detected in small-scale ecological experiments.

1.6 Figures

Figure 1.1 *Durvillaea* life cycle (adapted from Schiel and Forster (2006)).

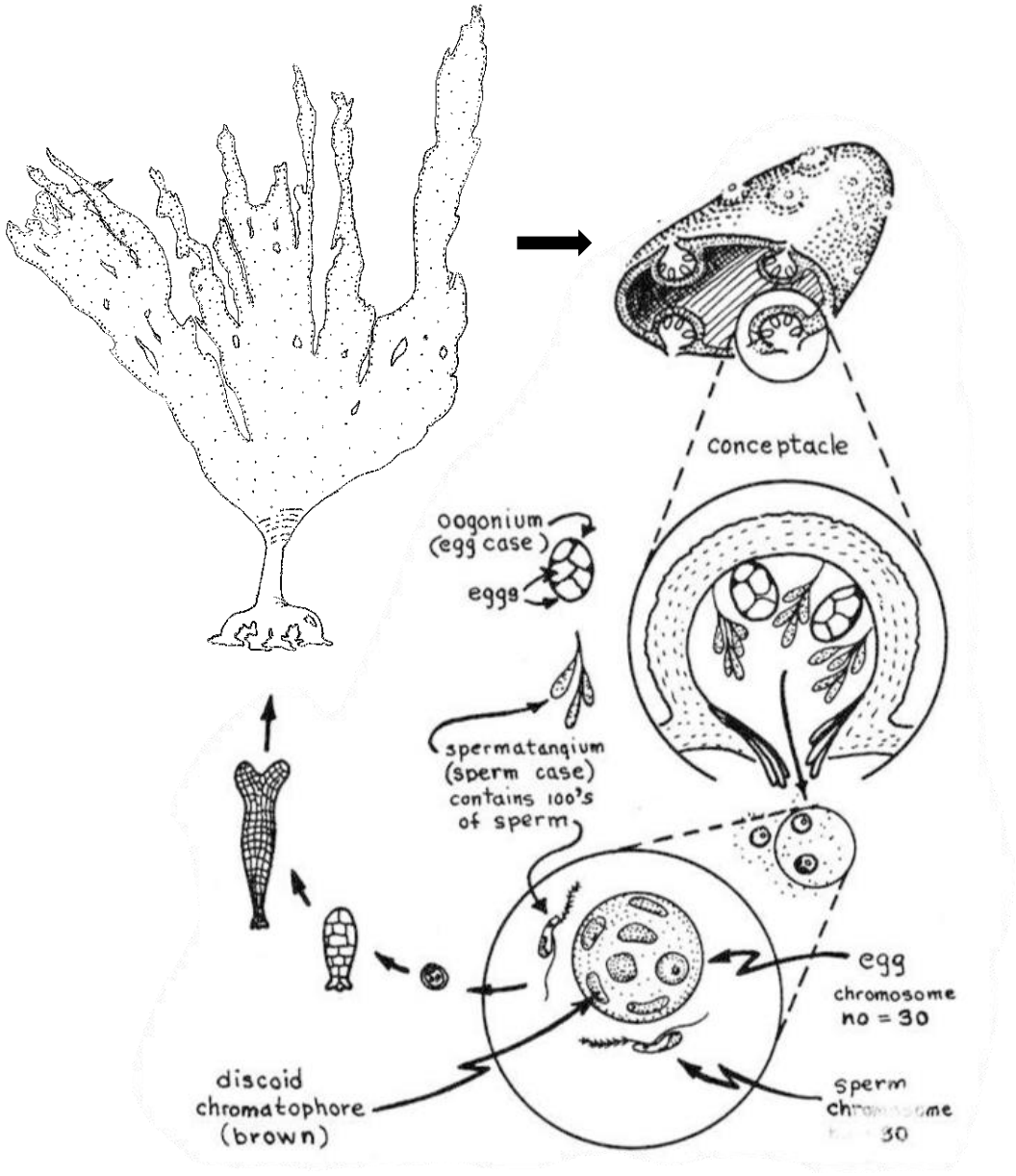
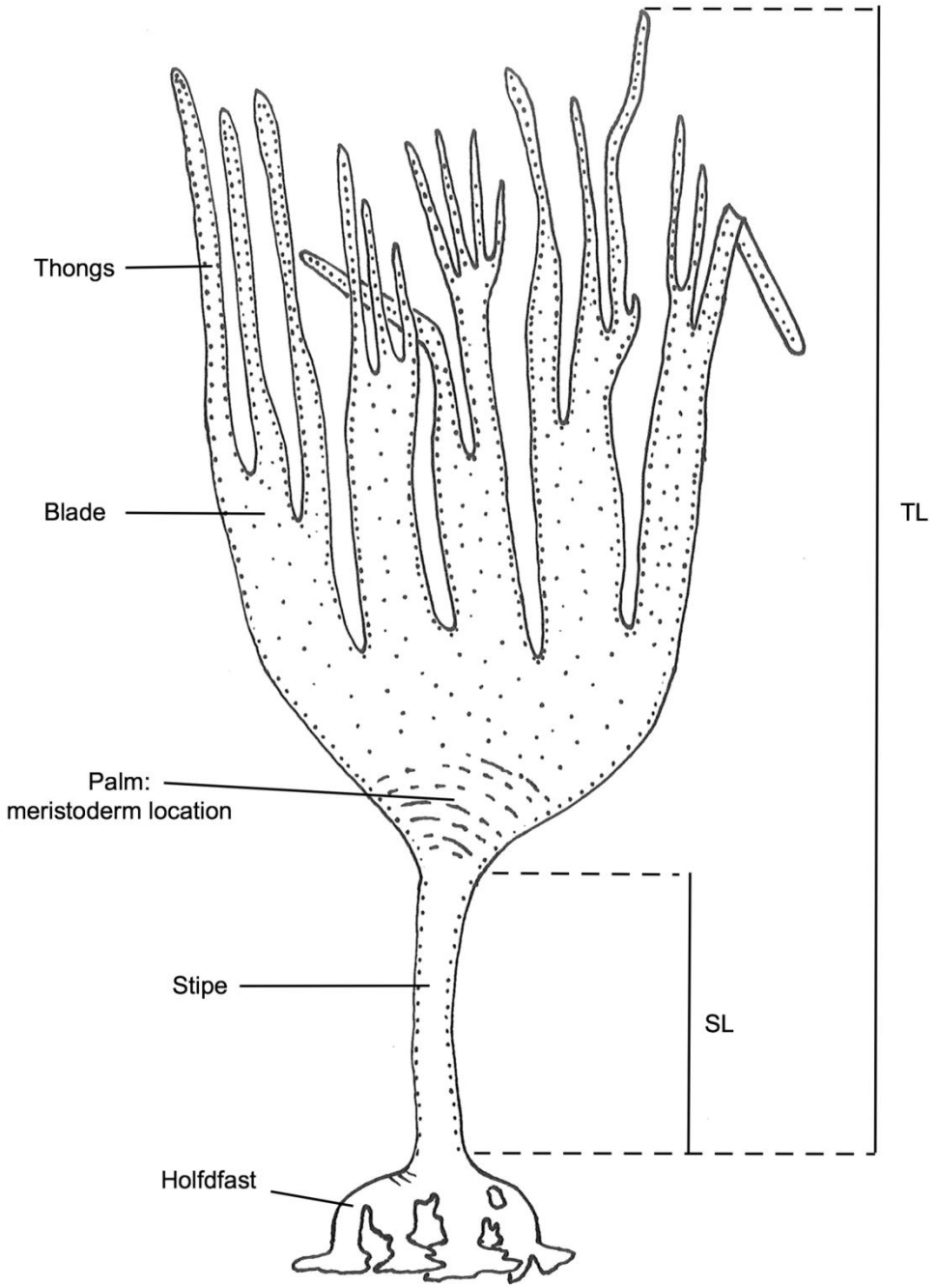
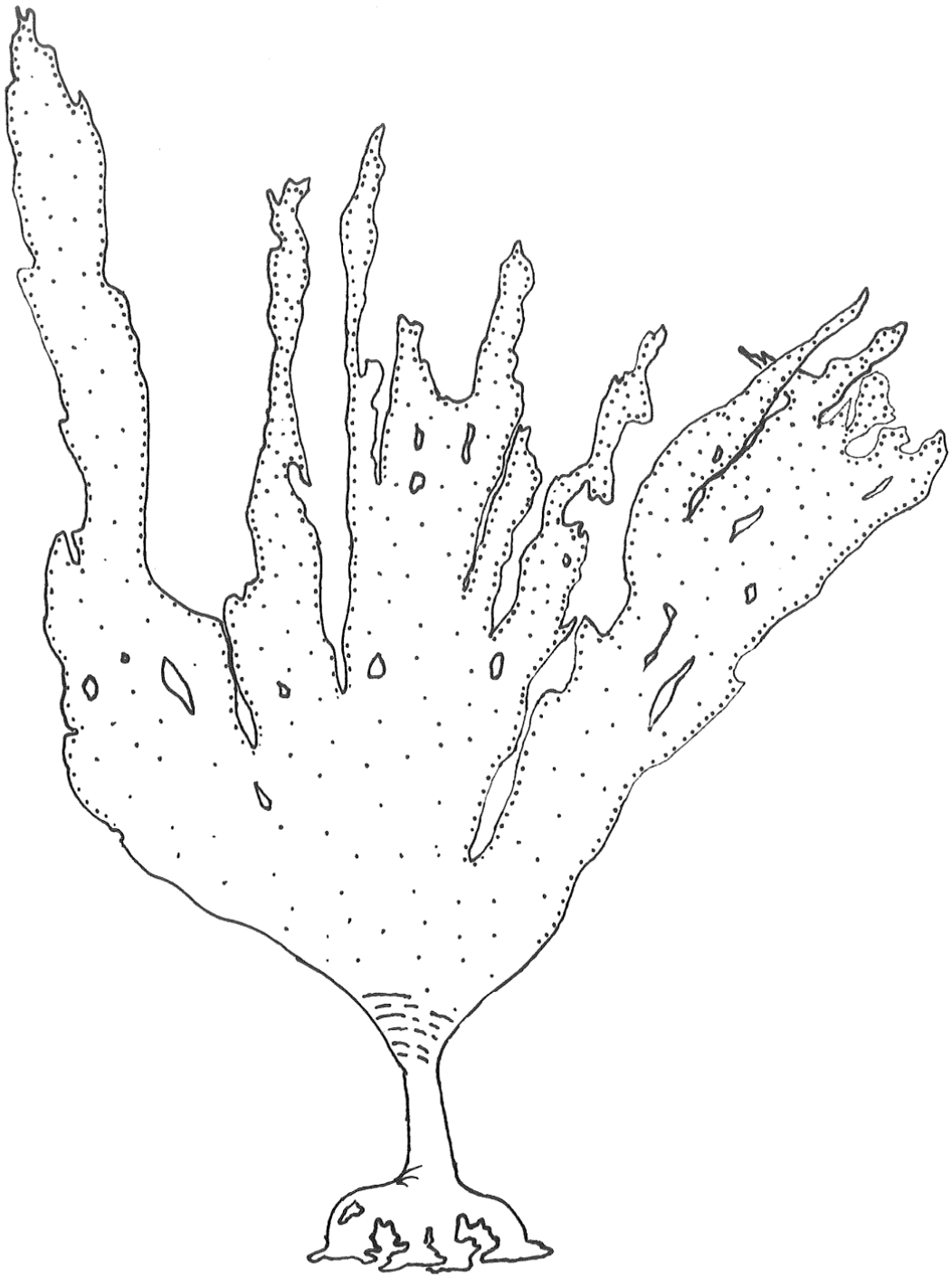


Figure 1.2 Morphology of typical *Durvillaea antarctica* (A) adapted from (Hay 1997), *D. poha* (B), and *D. willana* (C). TL = Total length, SL = Stipe length.

A.



B.



C.

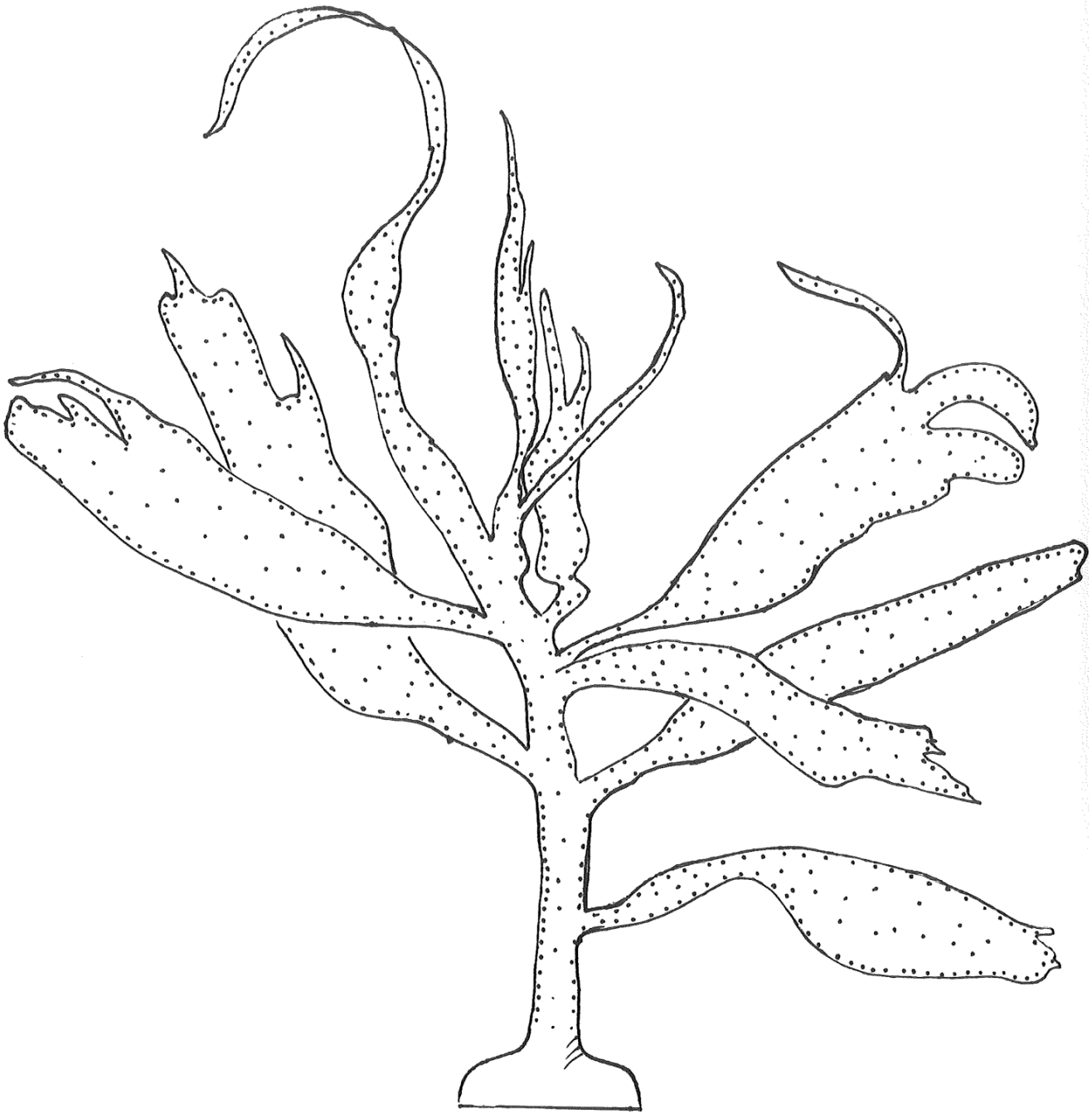


Figure 1.3 Map of New Zealand with major cities and study sites (bordered label). The uplifted coastline and the earthquake epicentre (star) are in red.

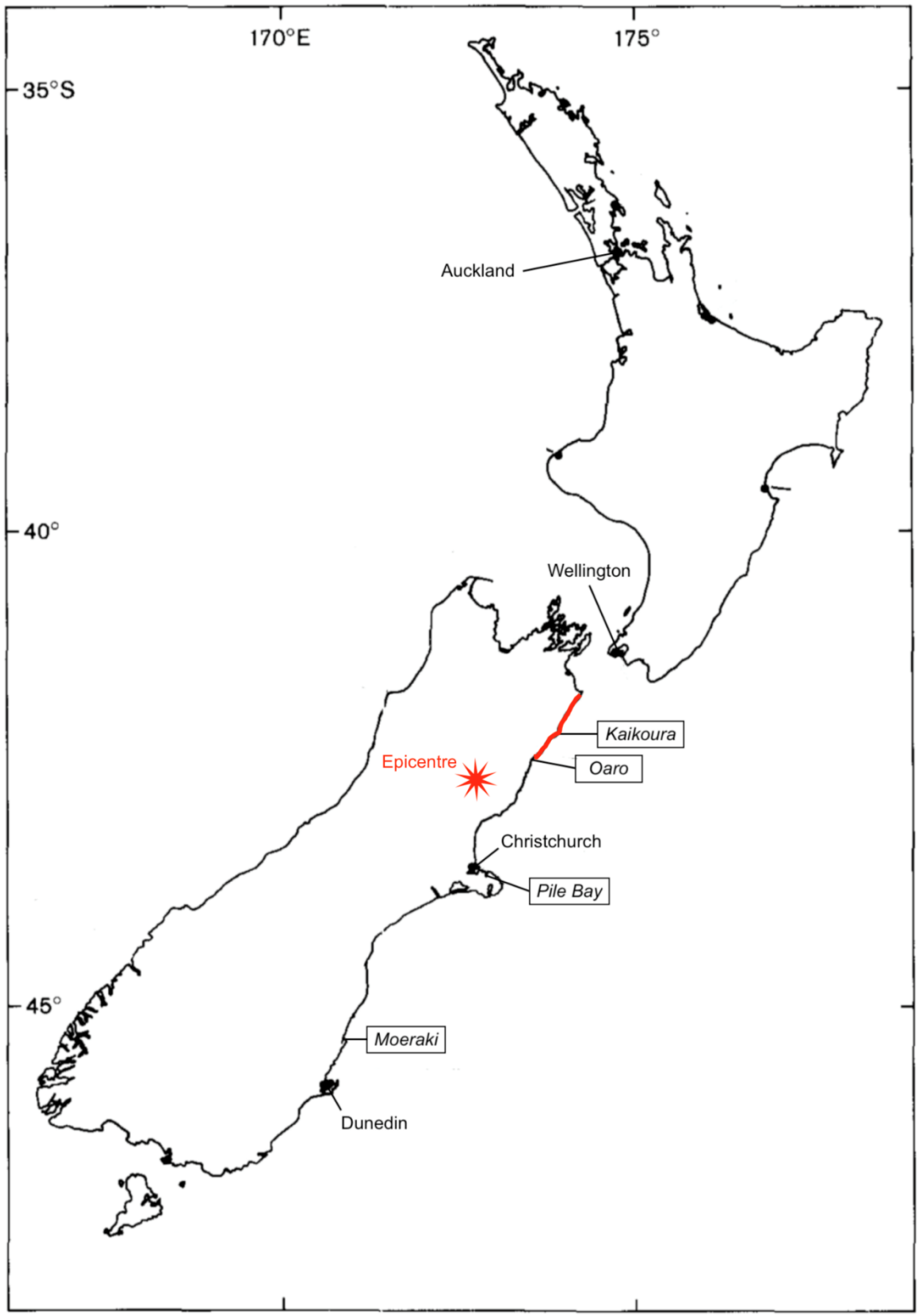
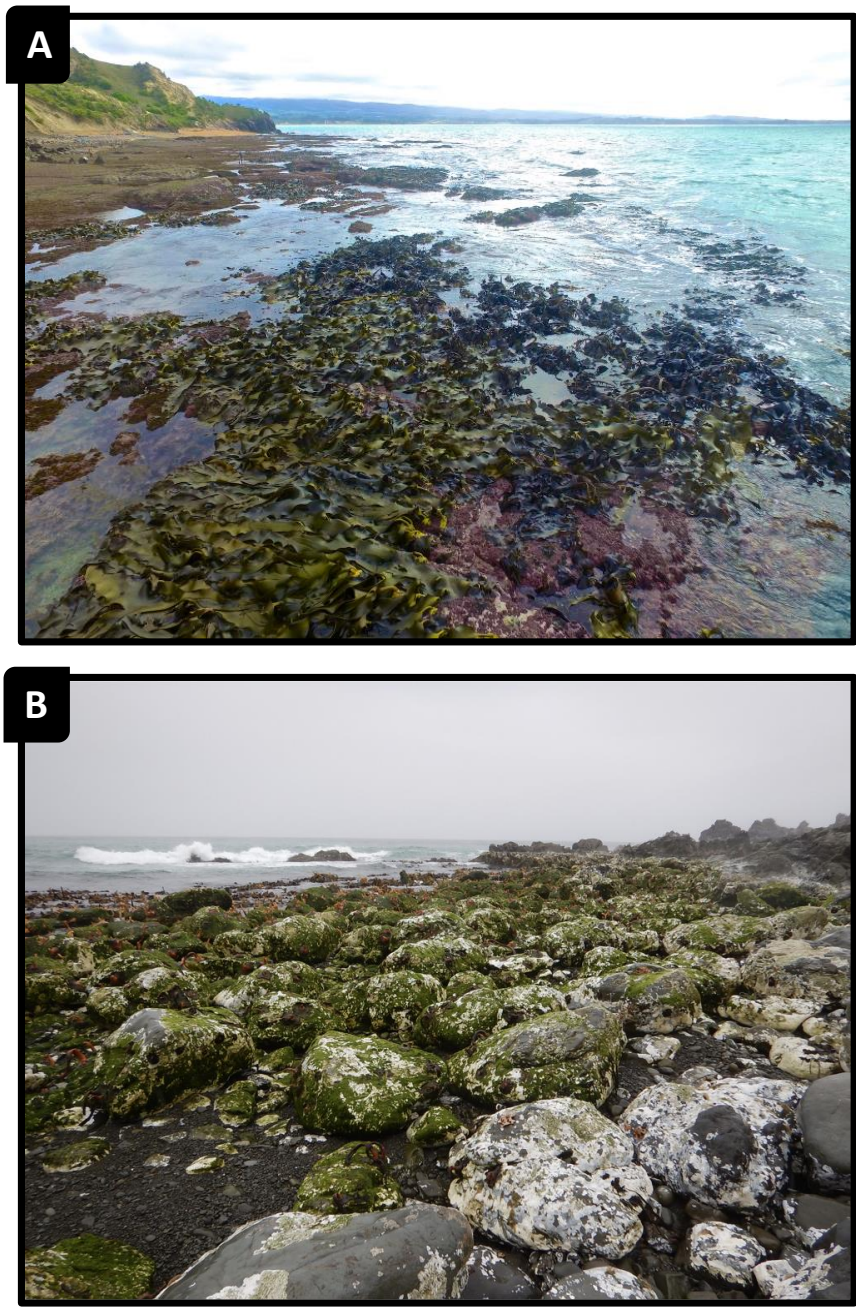


Figure 1.4 Photos of typical bull kelp habitat at Moeraki Point (A) and uplifted shore along the Kaikōura coastline (B).



Chapter 2:

Recovery of bull kelp following a gradient in disturbance intensities

2.1 Abstract

Large brown perennial seaweeds often control biodiversity and ecosystem functioning on many temperate wave-exposed rocky shores. During storms, they experience wave-disturbances of different intensities, ranging from pruning of their blades to removal of entire individuals. Although storm-disturbance is a fundamental driver of algae ecology, less is known about how they respond to disturbances of varying intensity. Here, I compared responses of adult and juvenile bull kelp (dominated by *Durvillaea poha* with a few interspersed *D. antarctica*), that dominates many wave-exposed rocky shores in the southern hemisphere, and two early colonizing seaweeds (the green alga *Ulva* spp. and the non-native kelp *Undaria pinnatifida*), between undisturbed control plots and three simulated disturbance intensities. To simulate a typical gradient in storm-disturbance effects, I removed either entire holdfasts, stipes or blades (cut 10 cm above the stipe-blade junction), at two reefs at Moeraki and one reef at Oaro on the South Island of New Zealand. Four months after these disturbances, in the stipe removal treatments, there were no major effects on density or sizes of adult holdfasts, demonstrating that after growth has ceased these biological structures can remain intact and attached to substratum. There were no disturbance-driven effects on either the density or the length of juvenile blades. Overall, juvenile densities were highly variable in space and time. I also found that the length of juvenile bull kelp increased in all treatments. In addition, most bull kelp with removed blades showed strong ability to recover, with new growing tips along the margins of cut tissue. Furthermore, all disturbed plots were colonized by either *Ulva* (Oaro) or *Undaria pinnatifida* (Moeraki). Finally, I found a negative correlation between the abundance of these early colonizers and the density of bull kelp recruits, indicating either that *Ulva* and *Undaria* inhibit new bull kelp recruitment or that the bull kelp recruits inhibit these colonizing seaweeds. My study shows that bull kelps are resilient to storm-disturbances, because they can recover from pruned blades or through formation of a new canopy from the growth of understory juveniles. However, when perennial kelps are lost, they are likely to be rapidly replaced by opportunistic seaweeds.

2.2 Introduction

Physical disturbances are fundamental structuring forces that affect local communities across a wide range of marine habitats (Sousa 1984, Englund and Cooper 2003, Schiel and Lilley 2011, Schiel et al. 2016). To better understand how these systems respond to disturbances,

many experiments have been carried out that compare entirely cleared plots to undisturbed control plots (De Loma et al. 2000, Edgar et al. 2004, Taylor and Schiel 2005, Schiel 2011, Schiel et al. 2018). However, in marine systems, disturbances occur over a wide range of intensities (Denny 1995), potentially resulting in complex population and community-wide effects that 'binary' control vs. clearance experiments cannot identify. In addition, disturbance effects may be context dependent and vary depending on local environmental conditions (Toohey et al. 2004, Taylor and Schiel 2005, Schiel 2006, Wernberg and Connell 2008, Schiel 2011).

Temperate reefs are often inhabited by large canopy-forming seaweeds (Schiel and Foster 1986, Steneck and Johnson 2014). More specifically, wave-exposed intertidal rocky reefs in the southern hemisphere, including the South Island of New Zealand, are often dominated by bull kelp species (*Durvillaea* spp., taxonomically these seaweeds are fucoids). These seaweed beds form complex ecosystems, supporting fish, invertebrate and algal communities as they control processes through blade abrasion and light reduction (Taylor and Schiel 2005, Wernberg et al. 2005, Irving and Connell 2006, Toohey et al. 2007). In addition, these seaweed beds also alter hydrodynamic flow conditions and key biological processes such as photosynthesis (Dayton 1985, Toohey et al. 2004, Tait and Schiel 2010), grazing (Konar 2000), and habitat availability (Anderson et al. 2005). Along rocky intertidal zones, kelp and fucoid canopies can modify this stressful habitat, characterized by strong waves and desiccation during low tide, into suitable sheltered habitat for many invertebrates and food for grazing fish like butterfish (*Odax pullus*) (Dayton 1985, Smith and Bayliss-Smith 1998, Taylor and Schiel 2005, 2010). Kelp can inhibit other large algae by whiplash effects from their large fronds, retain moisture on intertidal shores, and control nutrients and light availability (Taylor and Schiel 2005). On the other hand, where kelps have been lost or are highly stressed, for example by high temperatures or high grazing pressures, they can be replaced, at least for a short time, by a cover of small fast growing early colonizing algae (Estes and Duggins 1995, Graham 2004, Ling et al. 2009, Connell and Russell 2010, Wernberg et al. 2016, Schiel et al. 2018). In short, by creating a special habitat, characterized by rapid kelp growth, light flickering under the kelp canopy (Tait et al. 2014) and constant removals of sediments and abrasion of competitors and grazers, kelps and fucoids increase the overall biodiversity and productivity of coastal areas (Dayton 1985, Schiel and Foster 2015).

Many studies have simulated disturbances in simple clearance experiments, but much fewer experiments have tested how different disturbance intensities may affect recovery of large canopy forming seaweed (Schiel and Taylor 1999, Taylor and Schiel 2005, Schiel and Lilley 2007, Wernberg et al. 2010). Here, I address this research gap by conducting a field experiment which mimicked a disturbance gradient and compared undisturbed bull kelp plots to plots where blades were removed ca. 10 cm above the stipe-holdfasts junction (i.e., just above its growth meristem = low disturbance), plots where stipes were removed, (i.e. below its meristem = medium disturbance) and plots where entire holdfasts were removed (large disturbance). From this experiment, I tested the following hypotheses;

- bull kelp recovery is inversely related to disturbance intensity,
- adult bull kelp with blades removed will recover,
- adult bull kelp holdfasts with stipes removed will slowly degrade and therefore decrease in density and size,
- understory juvenile bull kelp, that may be limited by shading, will increase more in size and density in disturbed plots relative to undisturbed plots, and
- opportunistic seaweeds, that are, normally, outcompeted from blade shading and whiplash, will colonize disturbed plots.

2.3 Methods

A field experiment was conducted on three intertidal reef platforms, two reefs in Moeraki (-45.358119, 170.865734) and one in Oaro (-42.514561, 173.508112) on the South Island of New Zealand. These reefs are characterized by intermediate wave exposure levels and are dominated by wide-bladed *Durvillaea poha* and narrow-bladed *D. antarctica* (Fraser et al. 2012) in the lower intertidal zone. At each reef, 16 1 m^2 plots were established on reef sections covered by dense bull kelp, and randomly assigned to (1) undisturbed control plots, (2) plots were bull kelp blades were cut ca. 10 above the stipe-blade junction (above its growth meristem), (3) plots where most of the bull kelp stipe was removed (below its growth meristem) or 4) plots were all holdfasts were removed (i.e., recovery of individuals is impossible and more rocky substratum is freed up). Blades and stipes were removed with a knife and small and large holdfasts were removed from the reef with a chisel and crowbar, respectively. Juvenile bull kelp, here defined as bull kelp with a holdfast diameter smaller than 3 cm, were

left intact in all the plots, in part because small kelp are resilient to wave disturbances (Denny 1995, Denny 1999, Thomsen et al. 2004), in part because I was testing how these juvenile bull kelp respond to canopy removals. Each disturbance level was replicated four times at each of the three reefs.

The Moeraki plots were established in May 2017 and the Oaro plots in June 2017, that is, just before the peak in bull kelp reproduction season (Taylor and Schiel 2003, 2005). All plots were sampled again after four months. In each plot the following response variables were measured immediately before and four months after the disturbances: (1) number of holdfasts, (2) area of each holdfasts, (3) number of juveniles in the plots, (4) length of juveniles (up to 20 randomly selected juveniles), (5) sign of regeneration of cut stipes and blades (counted as 'new outgrowths', see Fig. 2.1) and percent cover of two common opportunistic seaweed species that typically live less than one year, that is (6) the green sheet-forming alga *Ulva* spp. and (7) the non-native Japanese kelp, *Undaria pinnatifida*. Due to time constrains and strong wave action, it was not possible to measure holdfast density and area in the control plots before the disturbances. However, because plots were allocated randomly within the bull kelp bed I assumed that the pre-disturbance conditions in these 12 unmeasured plots, on average, were similar to pre-disturbance conditions measured in the remaining 36 plots. Holdfast area of adult bull kelp was measured in ImageJ from photos taken perpendicular to each plot, each photo covering the whole quadrat.

2.3.1 Statistical analysis

Responses were analyzed with two-way ANOVA with disturbance treatment as a fixed factor and sites as a random factor. The holdfast removal treatment was excluded from the tests of holdfast density and sizes because their results were manipulated to be zero. Individual plots had different starting conditions and the four tests of holdfast and juvenile density and sizes were therefore analyzed on 'Difference' between the mean values per plot before and after disturbance treatments. 'Differences' were preferred over 'percent change' because some plots had no juveniles before (or after disturbances) making it impossible to calculate relative changes for all plots. The tissue regeneration response was analyzed graphically because only the blade removal treatment showed signs of strong recovery (see Results section). Percent cover of *Undaria*, *Ulva*, and the combined cover of *Ulva* and *Undaria* were analyzed with similar ANOVA's but only on the after-disturbance data because these species were absent in

all plots prior to removals. All bull kelp responses had homogeneous variances for both the Disturbance and Reef test factors (Levine's tests, $P > 0.05$). Percent cover data of colonizing opportunistic seaweed were arcsine transformed to reduce problems associated with variance heterogeneity. Significant results for the disturbance test factor were followed by SNK-post hoc tests. Finally, I investigated if early colonizing seaweed potentially inhibit juvenile bull kelp by correlating the combined cover of *Ulva* and *Undaria* vs. density and average length of juvenile bull kelp (again, only for the after disturbances results). Although these two-weedy species have very different traits, regarding phylogeny, life history, morphology, size and anatomy, I combined them in this correlation analysis in part because they colonized different reefs, in part because they both may inhibit small bull kelp recruits (e.g., by occupying primary substratum preventing new recruitment or by shading established small bull kelp recruits).

2.4 Results

There were no significant effects of disturbance treatments on the density of adult bull kelp holdfasts over the experimental period (Table 2.1, T1) with a net loss of 1.2 holdfasts per m^2 (± 0.4, data variability refer to one standard error here and in all following text, n = 36) across disturbance levels and reefs. Typical holdfast densities across plots were 8.2 (± 0.7) and 7.0 (± 0.5) before and after the disturbance treatments (Fig. 2.2A). However, there was a significant interaction between disturbance and reefs in changes to bull kelp holdfast sizes ($p = 0.047$, Table 2.1, T2). This interaction was complex and did not follow any obvious pattern related to disturbance intensities as three out of the 9 treatment-reef combinations showed a size reduction (Fig 2B, i.e., D_2 at Oaro, and D_0 and D_1 at Moeraki-K) whereas the other 6 combinations had a net increase in size (holdfast sizes from control plots were excluded because they were physically removed in treatment D_3). Overall, holdfast sizes were highly variable between sites and reefs, with typical values ranging from ca. 100 to 280 cm^2 (Fig. 2.2B)

There were no significant effects of either disturbances or reef on the densities of juvenile bull kelp (Table 2.1, T3). Densities varied greatly across plots (cf. large standard errors on Fig. 2.3A) with average densities ranging from ca. 2 to 40 bull kelp per m^2 (Fig. 2.3A). Finally, there were no significant effects of disturbances on the mean length of juvenile bull kelp (Table 2.1, T4). Generally mean bull kelp-length increased across all treatments from 14.79 (± 1.32, SE, n = 16) to 24.39 (± 2.91) cm over the experiment (Fig. 2.3B), although the net increase

differed among reefs ($p = 0.003$, Table 2.1, T4), with least growth at Oaro (1.63 ± 2.84 cm per juvenile bull kelp, n = 16), intermediate growth at Moeraki-K (6.43 ± 3.84) and highest growth at Moeraki-P (17.84 ±3.64).

Recovery of bull kelp blades occurred at all three sites with most blades showing new growth around the cut margins (Figs. 2.1, 2.4) although regrowth was lower at Oaro (ca. 55%) than the two Moeraki sites (ca. 85-90%). Interestingly, I also found a single stipe from Moeraki-P that showed similar new growth (Fig. 2.1, see discussion for detail).

Disturbed plots were colonised by *Undaria* at Moeraki (Fig. 2.5A) and *Ulva* spp. at Oaro (Fig. 2.5B). However, there was no significant effect of disturbance on *Undaria* cover in the 2-way ANOVA (Table 2.1, T5), probably because of high data variability and relatively low cover values (Fig. 2.5A). Still, a follow-up refined 2-way ANOVA, with Oaro data excluded (because there is no *Undaria* on that reef) and the three disturbance intensities reclassified to a single 'disturbance treatment' showed that *Undaria*, in this simpler analysis, was significantly more abundant in disturbed than undisturbed plots ($F_{1, 28} = 167.7$, $p = 0.049$). Finally, there was a significant interaction between disturbance and reef on the cover of *Ulva* spp. (Fig. 2.5B, Table 2.1, T6), demonstrating that *Ulva* only colonized disturbed plots at Oaro, but not Moeraki sites. The post hoc SNK test showed that the three disturbed plots had higher *Ulva* cover compared to the control.

Finally, I found strong negative correlations between the combined cover of *Undaria* and *Ulva* and density ($r = -0.414$, $p = 0.003$, n = 48, Fig. 2.6A) but not length ($r = -0.062$, $p = 0.677$, n = 48, Fig. 2.6B) of juvenile bull kelp.

2.5 Discussion

This experiment showed that bull kelp can recover from different intensities of small localized disturbances (within a square meter) either through new growth of blades that have been pruned or by the rapid growth of understory juveniles. My results also highlight that holdfasts left only with a stipe can persist almost unchanged for at least four months which is, potentially, of high importance for the many invertebrates that depend on this specialized habitat (see Chapter 3). I also found that the fast-growing seaweeds *Undaria* and *Ulva* successfully colonized almost all disturbed plots. Their presence may potentially slow down recovery or even change the

coastal environment permanently if the damage is spatially and temporally more extensive (e.g., Chapter 4).

2.5.1 Impact on bull kelp holdfasts

In contrast to my hypothesis, I found no decrease in holdfast size or density up to four months after blades and stipes were removed. This is important because many kelp removal studies ignore effects of holdfasts and mainly focus on effects on the understory communities after complete canopy removals (Grime 1977, Kennelly 1987b, Wernberg 2006, Wernberg and Connell 2008). It is possible that results from these other studies would have been different if holdfasts had been left intact. For example, in other studies were holdfasts were left intact, Westermeier et al. (1994) described relatively stable large holdfasts of *D. antarctica* while smaller holdfasts showed stronger seasonality, but eventually with high mortality occurring over a 3 year period. Similar conclusions were also highlighted by Hay (1977) who recorded a loss of all holdfasts after 12-16 months after the stipes were severed. Finally, my results are also supported by the persistent holdfast observed along the Kaikōura coastline on uplifted reefs following a large earthquake where bull kelp holdfast remained attached to the reef for many months without any blades (see Chapter 3). I do expect, though, that over the next few years all holdfast with cut stipes will slowly deteriorate (i.e., with decreases in sizes) and eventually break off entirely from the substratum (i.e., with decreases in densities). Persistent holdfasts may be of some potential ecological importance for invertebrate fauna that lives inside holdfast (see Chapter 2) as these organisms then may have time to colonise adjacent bull kelp (in case the holdfasts slowly decrease in sizes).

2.5.2 Impact on bull kelp recruits

By removing most of the blade and thereby associated blade whiplash and shading effects, I expected to find a high recruitment and increase in length of understory juvenile kelp (Hay 1977, Ebeling et al. 1985, Kennelly 1987b, a, Cheshire and Hallam 1988, Wernberg et al. 2010). However, I did not find support for this hypothesis, perhaps because different processes following blade removal can either inhibit (e.g., because of colonizing grazers and competitor) or facilitate (e.g., because of less shading and abrasion) recruitment and growth of juvenile kelp, thereby creating high variability in juvenile kelp data. For example, Wernberg et al. (2010) found that kelp canopies facilitate juvenile kelp in warmer (stressful) waters but inhibit juveniles in colder waters. Other complex kelp recruitment patterns were reported by Taylor

and Schiel (2005) who over a longer period found high variability in juvenile responses between different years, season of clearings, and geographical areas. I aimed to maximize the available time for recruitment and net growth by initiating disturbance treatments in May at the start of the reproductive season (Westermeier et al. 1994, Taylor and Schiel 2005). The large variability in my results is perhaps not that surprising, considering the relatively short duration of the experiment and past research on kelp recruitment (Reed and Foster 1984, Reed 1990, Taylor and Schiel 2005, Wernberg and Connell 2008, Carnell and Keough 2014). For example, Taylor and Schiel (2005) also found variable recruitment in *Durvillaea* between sites, seasons and clearance treatments, but with a pattern of highest recruitment in experimental clearances (particularly were coralline understory alga were also removed). Still, my results are relatively similar to the results obtained by Taylor and Schiel (2005) from their autumn/winter clearings with comparable length data. In addition, Hay (1977) also reported similar rapid growth of juvenile plants when adults were removed.

2.5.3 Blade recovery

In support of my hypothesis, blades cut above the meristem generally showed sign of recovery, as shown previously for bull kelp (Hay 1977, Westermeier et al. 1994, Taylor and Schiel 2005). More specifically, I observed that stipe and blade removal treatments followed the regeneration and fading patterns described in detail by Westermeier et al. (1994). Although the duration of my experiment was much shorter than Westermeier et al. (1994), similar regeneration of blades was found on all three reefs. I also found a few single cut stipes with similar regrowth (Fig. 2.1) suggesting that this individual may actually recover. However, Hay (1977) noted a similar pattern of initial regrowth on a few stipes, but these stipes ultimately decayed and died, suggesting that initially after a cut growth may occur through translocated carbon, but that this cannot be sustained for long.

2.5.4 Colonization by Ulva and Undaria

It is well established that removal of macroalgal canopies can have dramatic and rapid effects on understory species (e.g. Sousa 1984, Kennelly 1987a, b, Taylor and Schiel 2005, Wernberg and Connell 2008, Schiel and Lilley 2011, Flukes et al. 2014). Many studies have shown rapid colonization by turf-forming algae that can limit new recruitment by canopy forming seaweeds (Dayton et al. 1984, Kennelly 1987a, Reed 1990, Schiel and Lilley 2011). Studies in Australia, however, have shown that kelp removals also can lead to shifts in other canopy forming species,

like *Sargassum* spp. and *Cystophora* spp. (Kendrick et al. 2004). Space occupation, shading effects, and potentially hosting of small grazers that consume juvenile kelp are some of the reasons why turfs may limit new kelp recruitment (Dayton et al. 1984, Reed 1990, Schiel et al. 2006). In addition, Kennelly (1987a) proposed that turf forming algae may also have an allelopathic function, by chemically modifying the substrate and potentially inhibit kelp recovery even after turfs are removed. Finally, many studies have shown that the non-native kelp, *Undaria* is an efficient colonizer of disturbed reefs (Valentine and Johnson 2003, 2004, Raffo et al. 2009, Schiel and Thompson 2012, Thompson and Schiel 2012, Carnell and Keough 2014, South and Thomsen 2016) and in particular so for reefs dominated by bull kelp (Schiel et al. 2018). My experiment supports these findings but with the added notion that 'propagule' pressure' can have a strong modifying effect of what type of early colonizers arrive because *Undaria* was absent from Oaro whereas *Ulva* was relatively rare at Moeraki (pers. obs). These two species are fast-growing and relatively short living, but whereas *Ulva* only grows to 20-30 cm *Undaria* can reach >1 m in a few months, potentially resulting in dramatically different types of habitats. Interestingly, I found a negative correlation between the abundance of these early colonizing species and bull kelp recruits, suggesting either that these seaweeds can inhibit juvenile bull kelp at least on short time scales, and/or that the juvenile bull kelp reduce recruitment of *Undaria* and *Ulva*. Still, longer-term experiments suggest that, without any further stressors, kelp will eventually recover and outcompete the annuals through whiplash and shading effects (Kennelly 1987b, Dayton et al. 1992, Schiel et al. 2018).

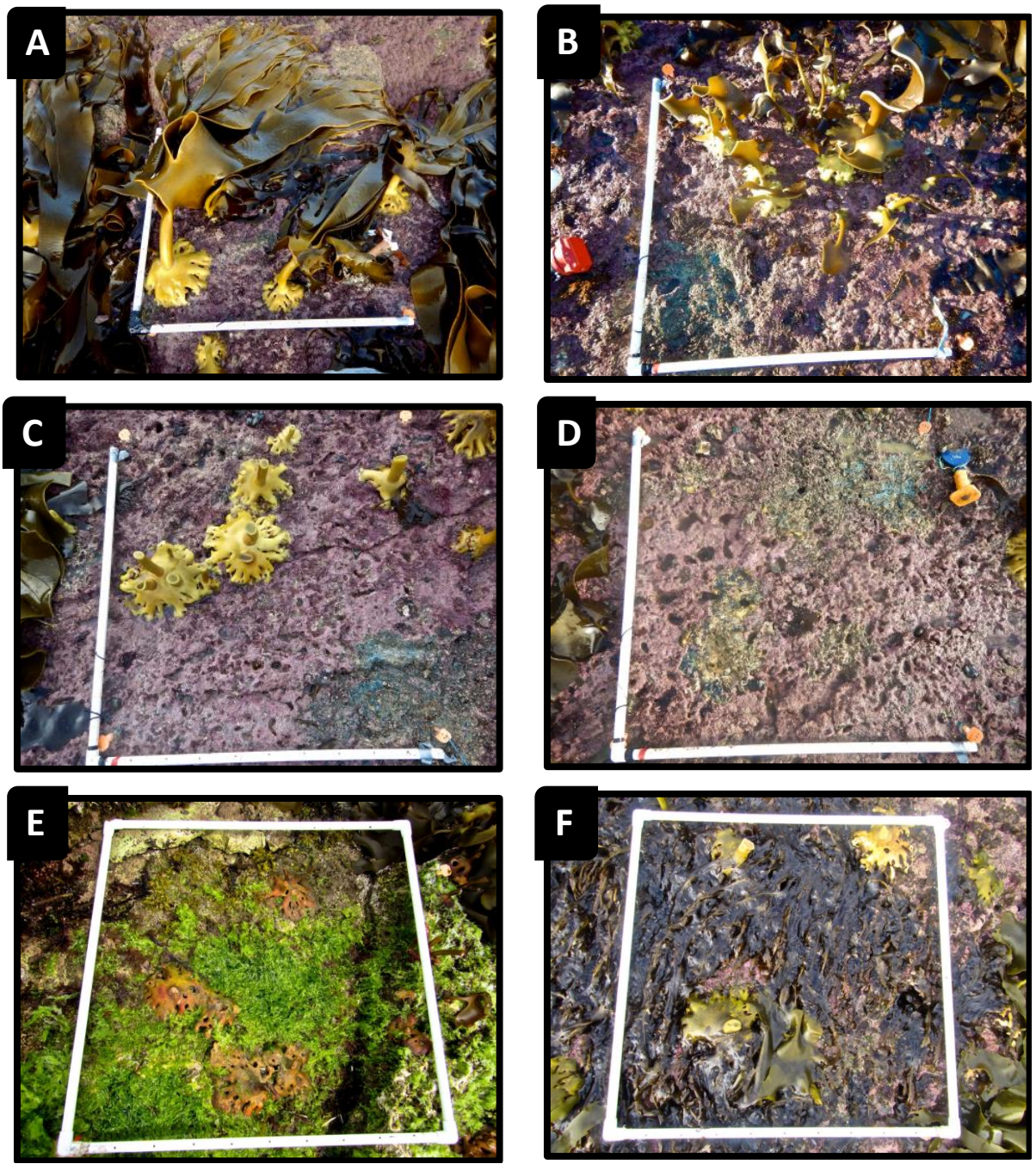
2.5.5 Conclusions

In conclusion, my experiment suggests that bull kelp can recover from localized storm-disturbances through regrowth of pruned blades and/or by rapid growth of juvenile bull kelp existing below the canopy. Furthermore, annual fast-growing seaweed, like *Ulva* and *Undaria*, are normally absent from dense bull kelp forests, but can rapidly colonize disturbed plots and may thereby co-exist with bull kelp when and where storms regularly remove patches of bull kelp.

Table 2.1 Anova. Effects of disturbances (fixed factor) across reefs (random factor) on changes in bull kelp holdfast density (T1), holdfast area (T2), juvenile density (T3), juvenile length (T4) and on cover of the colonizing seaweed *Undaria* (T5) and *Ulva* (T6) four month after the experiment was initiated. All bull kelp data (T1-T4) had homogeneous variances whereas cover data were arcs square root transformed. Significant results ($p < 0.05$) are in bold.

Test	Factor	Variability	SS	Df	F	p
T1	Disturbance (D)	Hypothesis	14.39	2	5.45	0.072
HF		Error	5.28	4		
Density	Reef (R)	Hypothesis	0.22	2	0.08	0.921
		Error	5.28	4		
	D × R	Hypothesis	5.28	4	0.26	0.904
		Error	139.75	27		
T2	Disturbance (D)	Hypothesis	5452	2	0.37	0.711
HF		Error	29275	4		
Area	Reef (R)	Hypothesis	4	2	0.00	1.000
		Error	29275	4		
	D × R	Hypothesis	29275	4	2.79	**0.047**
		Error	70913	27		
T3	Disturbance (D)	Hypothesis	3783	3	1.49	0.309
Juv.		Error	5065	6		
Density	Reef (R)	Hypothesis	73	2	0.04	0.958
		Error	5065	6		
	D × R	Hypothesis	5065	6	1.40	0.243
		Error	21783	36		
T4	Disturbance (D)	Hypothesis	257	3	1.34	0.347
Juv.		Error	384	6		
Length	Reef (R)	Hypothesis	2230	2	17.42	**0.003**
		Error	384	6		
	D × R	Hypothesis	384	6	0.29	0.939
		Error	7983	36		
T5	Disturbance (D)	Hypothesis	4129	3	3.130	0.109
Undaria		Error	2638	6		
	Reef (R)	Hypothesis	5869	2	6.674	**0.030**
		Error	2638	6		
	D × R	Hypothesis	2638	6	0.695	0.656
		Error	22792	36		
T6	Disturbance (D)	Hypothesis	2579	3	1.146	0.404
Ulva		Error	4501	6		
	Reef (R)	Hypothesis	14514	2	9.673	**0.013**
		Error	4501	6		
	D × R	Hypothesis	4501	6	4.395	**0.002**
		Error	6145	36		

Figure 2.1 Photos. A = undisturbed plot (D_0), B = blades removed ca. 15 cm above the stipe-blade junction (D_1), C = stipe removed (D_2), D = holdfast removed (D_3). E = *Ulva* colonized D_2 plot at Oaro, F = *Undaria* colonized D_2 plot at Moeraki, G = new growth (dentations) on the margin of cut blade, H = new growth on the margin of cut stipe, I = Moeraki-P bull kelp reef, J = single 3 cm tall juvenile bull kelp. Quadrats size = $1m^2$



Continue from Figure 2.1.

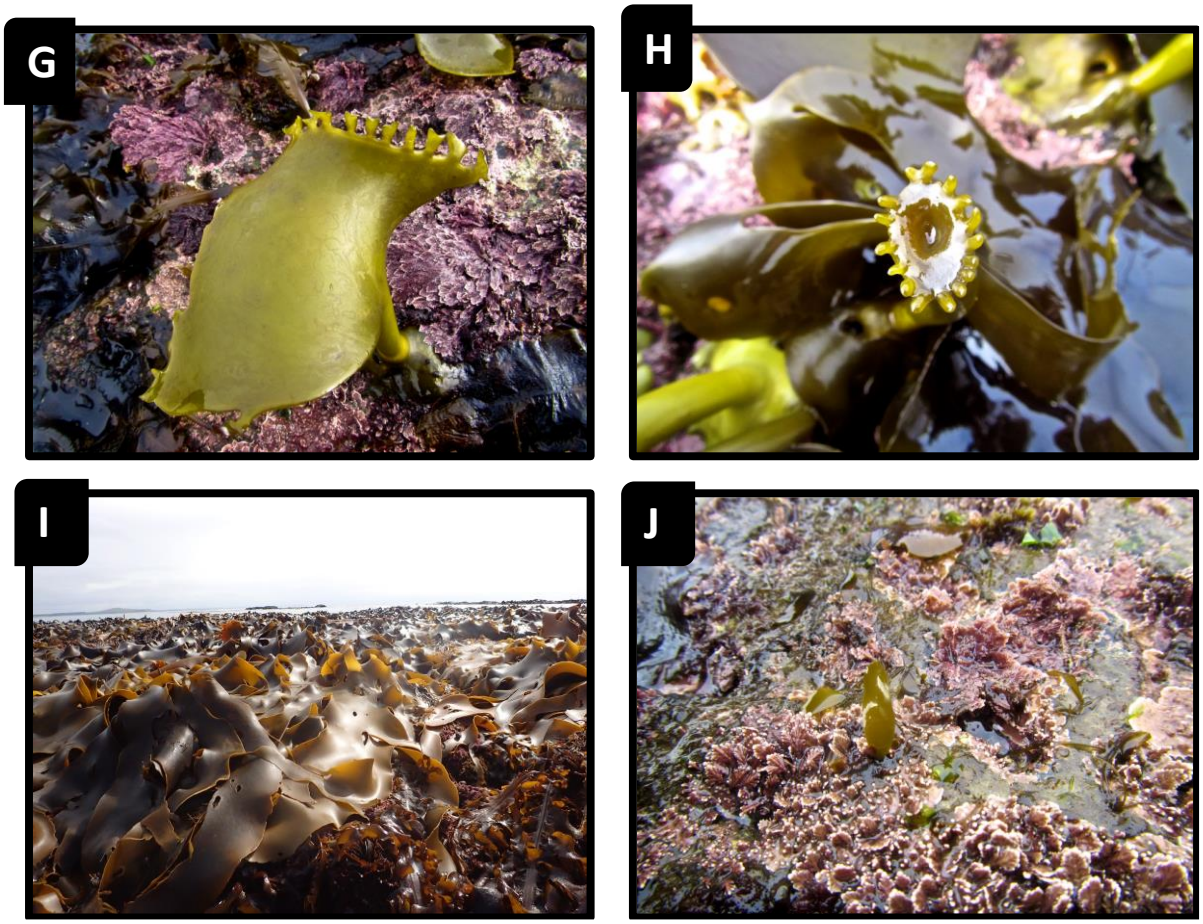


Figure 2.2 Densities (A; counts) and average sizes (B: cm^2 area) of bull kelp holdfasts in 1 m^2 plots from 'Moeraki-K', 'Moeraki-P', and 'Oaro', before (T_0) and after (T_1) four simulated disturbance regimes; nothing removed in control plots (Open bars = D_0), blades removed 5-10 cm above the meristem (Light grey bars, D_1), stipe removed from its mid-section (Dark grey bars, D_2) and entire holdfasts removed (Black bars, D_3) (n = 4, error bars are SE).

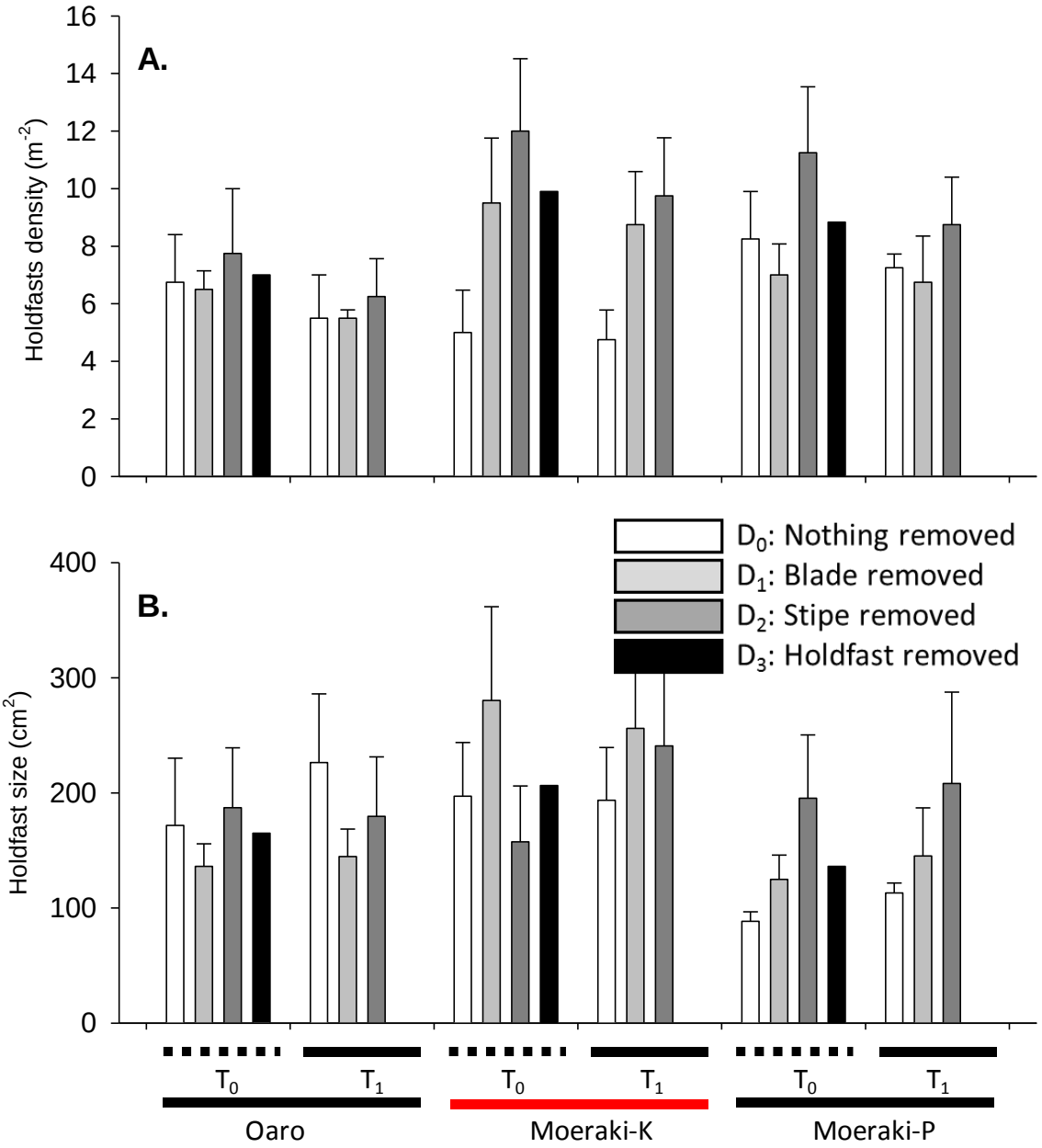


Figure 2.3 Densities (A; counts) and average sizes (B: cm length) of juvenile bull kelp in 1 m^2 plots from 'Moeraki-K', 'Moeraki-P', and 'Oaro', before (T_0) and after (T_1) four simulated disturbance regimes; nothing removed in control plots (Open bars = D_0), blades removed 5-10 cm above the meristem (Light grey bars, D_1), stipe removed from its mid-section (Dark grey bars, D_2) and entire holdfasts removed (Black bars, D_3) (n = 4, error bars are SE).

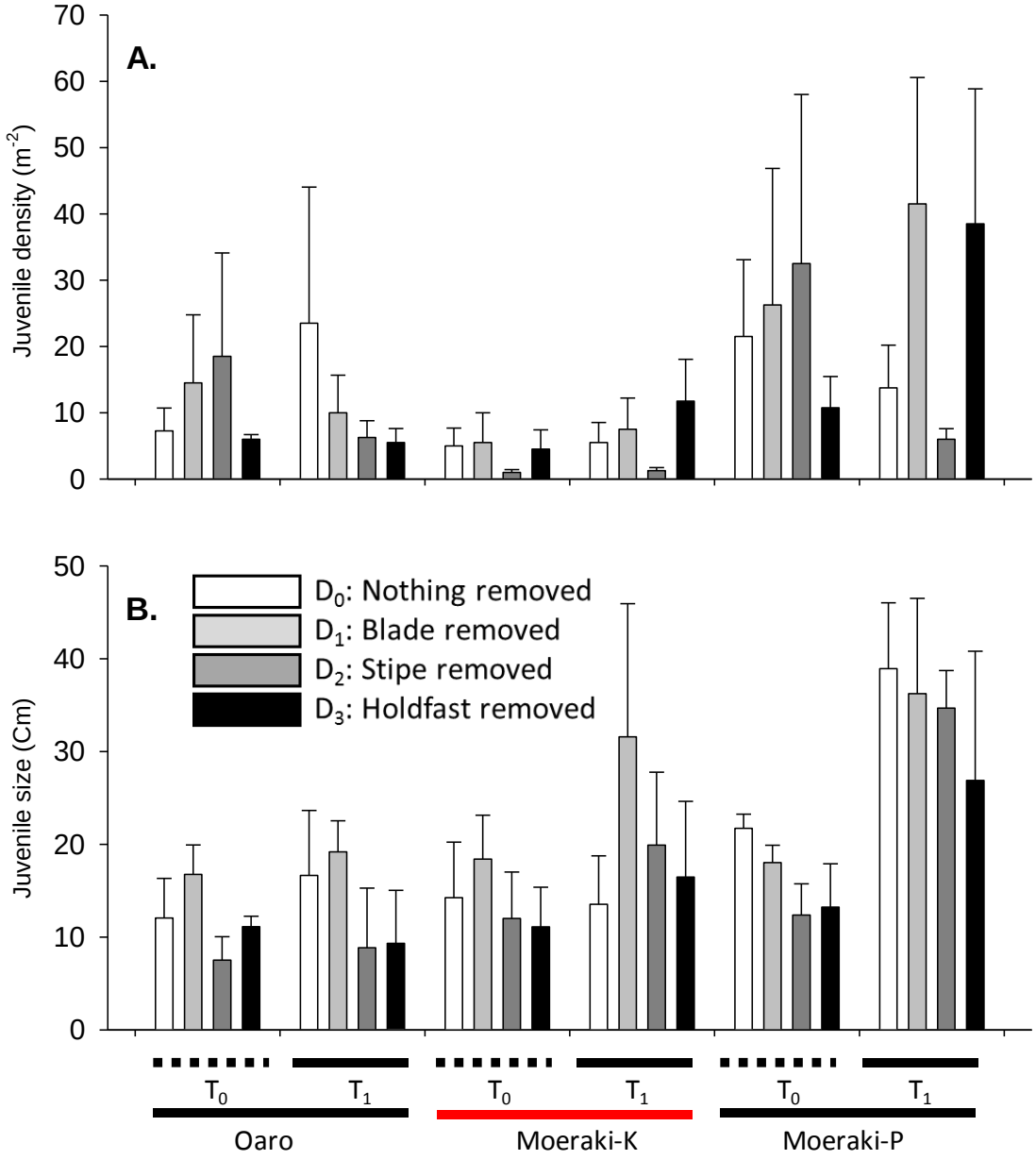


Figure 2.4 Recovery and tissue regeneration (A; percent) of bull kelp in 1 m^2 plots from 'Moeraki-K', 'Moeraki-P', and 'Oaro', before (T_0) and after (T_1) four simulated disturbance regimes; nothing removed in control plots (Open bars = D_0), blades removed 5-10 cm above the meristem (Light grey bars, D_1), stipe removed from its mid-section (Dark grey bars, D_2) and entire holdfasts removed (Black bars, D_3) (n = 4, error bars are SE).

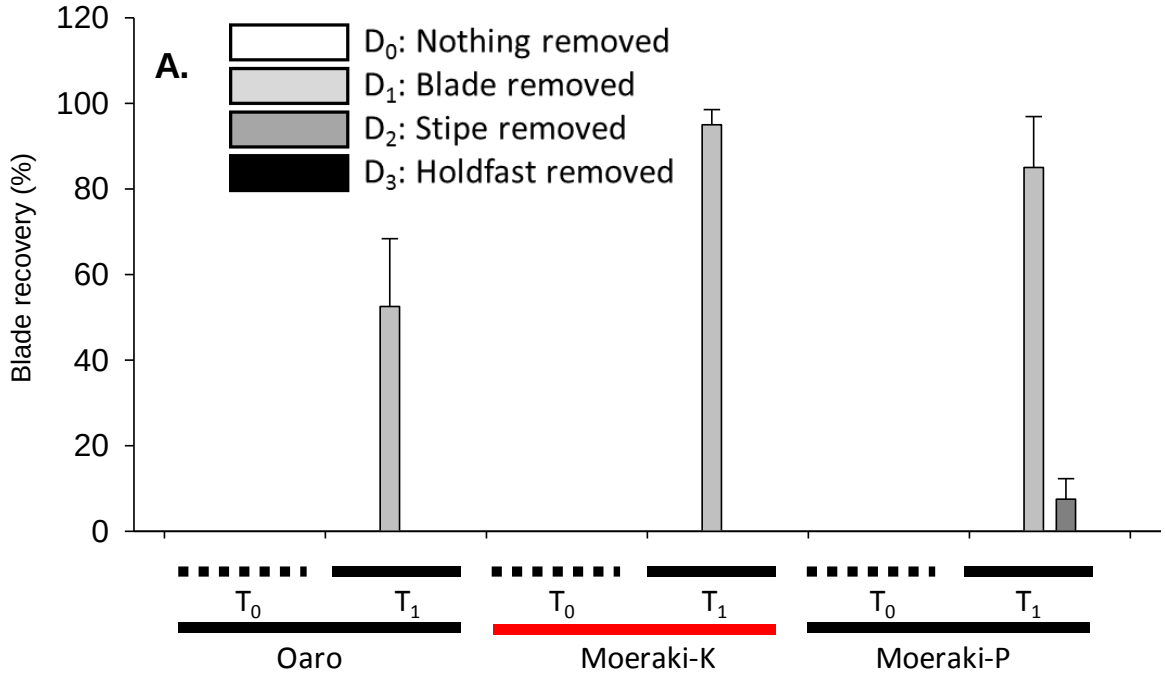


Figure 2.5 Abundance (percent cover) of *Undaria pinnatifida* (A) and *Ulva* spp. (B) in 1 m^2 plots from 'Moeraki-K', 'Moeraki-P', and 'Oaro', before (T_0) and after (T_1) four simulated disturbance regimes; nothing removed in control plots (Open bars = D_0), blades removed 5-10 cm above the meristem (Light grey bars, D_1), stipe removed from its mid-section (Dark grey bars, D_2) and entire holdfasts removed (Black bars, D_3) (n = 4, error bars are SE).

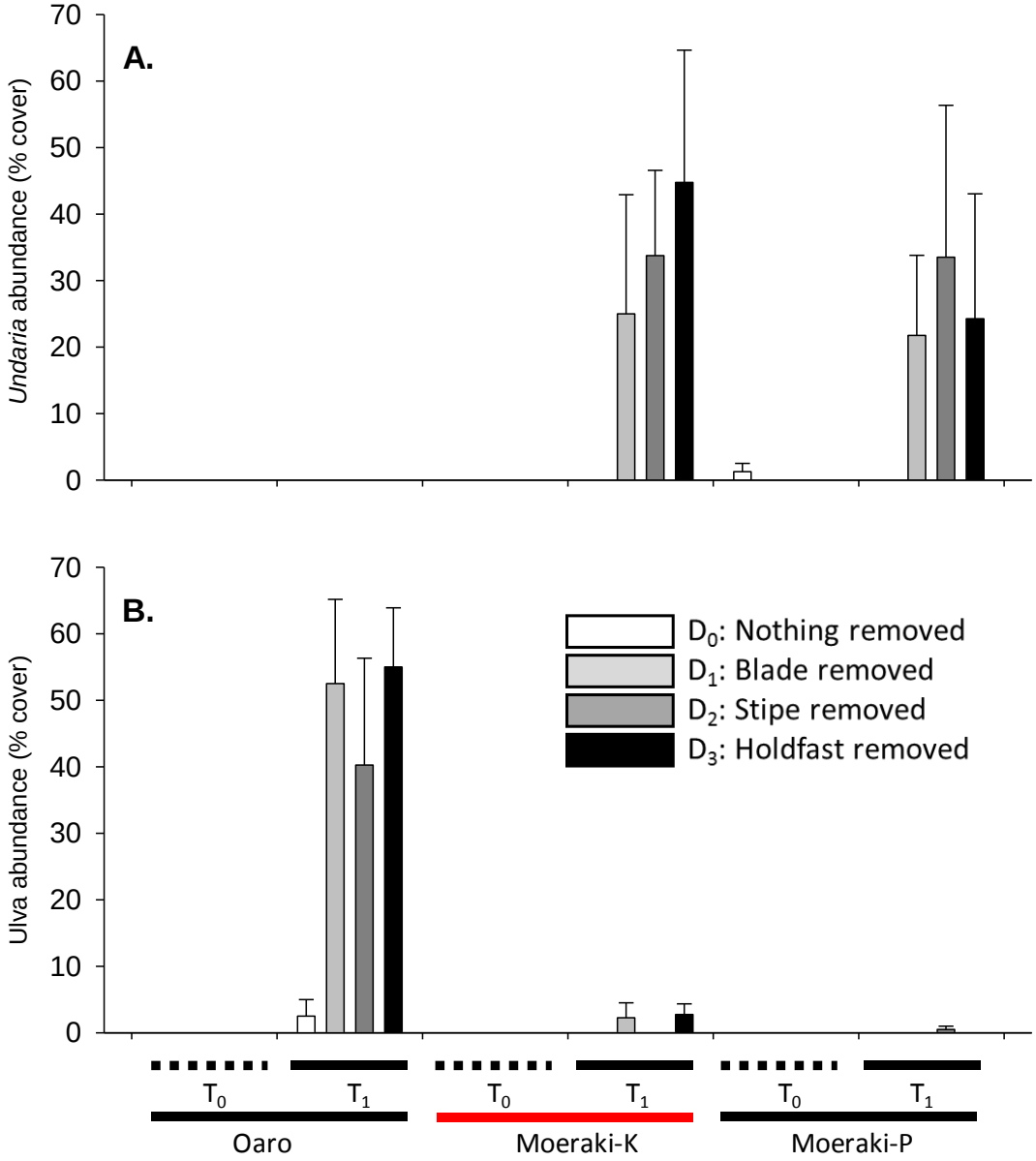
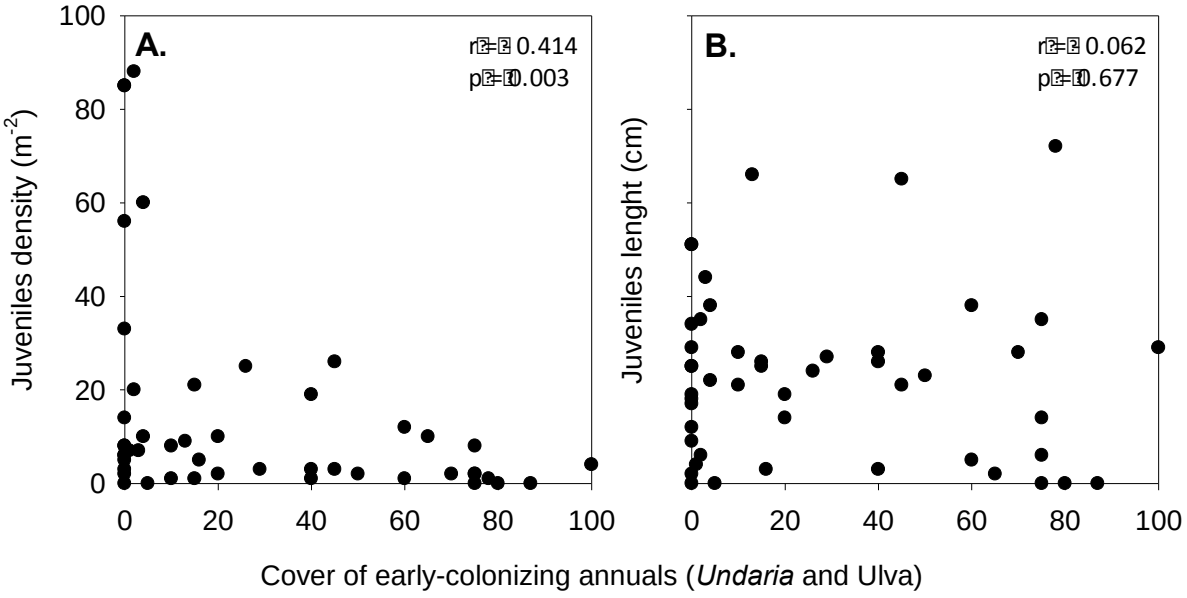


Figure 2.6 Correlations between cover of early colonizing algae (*Undaria* and *Ulva* combined) and the density (A) and length (B) of juvenile bull kelp (4 month after disturbances were initiated, there were no *Undaria* or *Ulva* in any plots prior to the disturbances).



Chapter 3: Bull kelp holdfasts as invertebrate habitat

3.1 Abstract

Bull kelp (*Durvillaea* spp.) are ecologically important large brown seaweeds that often dominate on wave-exposed rocky shores in the southern hemisphere. Bull kelp are firmly attached to the rocky substratum by a large holdfast that can survive up to 10 years. Bull kelp holdfast create, like large kelp holdfasts, habitat for benthic invertebrates. Because of their insular characteristics, small sizes, and complex morphology, holdfasts have been used as a model system to identify habitat attributes that support high biodiversity. Here, I first collected *Durvillaea poha* holdfasts to test if holdfast-associated invertebrates differ between different sites located along a latitudinal gradient in the South Island of New Zealand and between different holdfast sizes. This survey showed no differences in abundances of dominant taxa (crustaceans and gastropods) between sites, although more taxa and higher abundances of less dominant taxa were found at mid-latitude sites. In addition, larger holdfasts had, as expected, more invertebrates than small holdfasts. I then used a factorial short-term transplant experiment to test if colonizing invertebrates differed between different holdfast morphologies (round vs. elongated shapes), holdfast types (live holdfast vs. 3D printed abiotic models) and holdfast species (*Durvillaea poha* vs. the fast-growing non-native kelp *Undaria pinnatifida*). I found, for similar-sized holdfast, that more invertebrates were associated with live than abiotic holdfasts and with *Undaria* compared to *Durvillaea* (but with no effects of holdfast shape). These results suggest that invertebrates may partially consume holdfasts, or, perhaps more importantly, depend on small interstitial spaces associated with highly complex biological structures. Although *Undaria* supported more invertebrates than bull kelp of similar sizes, the *Undaria* habitat is, however, both more ephemeral (because it persists for less than one year compared to up to 10 years for bull kelp) and typically much smaller. I conclude that when bull kelp holdfasts are lost in storms, through natural extreme events, or through anthropogenic stressors, the rich fauna that inhabit the holdfast is then either lost from the system or has to rapidly abandon the holdfasts and, to avoid predation, immediately locate and colonize a new nearby analogy habitat.

3.2 Introduction

Bull kelps (*Durvillaea* spp.) are large habitat formers and modifiers throughout much of cool temperate Australasia and South America on wave exposed intertidal rocky reefs. Also known as ‘foundation species’, these organisms allow by virtue of their structure a suite of species to

inhabit stressful environments (Bruno and Bertness 2001, Stachowicz 2001). Bull kelps support high local primary productivity, attenuate waves and provide food for grazing fish and habitat for invertebrates (Steneck et al. 2002, Taylor and Schiel 2005, 2010). Each individual is composed of a holdfast (the structure that attaches to the rocky substratum), a large flexible buoyant blade (that provides most of the photosynthetic area) and a stipe (a flexible very strong structure that connects the blade and holdfast). Bull kelp can grow to 10 m long, live up to 10 years, and provide extensive biomass (up to 80 kg/m^2) to rocky intertidal areas (Taylor and Schiel 2005, 2010). Only a few epiphytes and mobile invertebrates inhabit the stipe and blades because they have smooth surfaces that constantly move in the wave-exposed surf zone, where they are whiplashed by neighbouring blades and rocks. By contrast, the holdfast, as shown for different kelp species, supports a novel habitat for many invertebrates (McLay and Hayward 1987, Anderson et al. 1997, Anderson et al. 2005, Taylor and Schiel 2005). These invertebrate species typically colonize the underside of the holdfast in cavities between tissue and rocks, where they find food and protection from predators, desiccation, wave action and whiplash (McLay and Hayward 1987, Smith and Simpson 1995, Smith 2000, Smith and Simpson 2002). Because kelp holdfasts are individual and isolated complex biogenic structures that provide habitat to many small animals, these structures have been considered independent 'micro-landscape units' (Edgar and Burton 2000, Anderson et al. 2005, Hauser et al. 2006, Tuya et al. 2011) and have been used to test ecological questions related to landscape size, configuration, density, isolation, and age, as well as how these landscape metrics are affected by human and natural stressors. More generally, kelp holdfasts are therefore considered useful model systems to test hypotheses related to landscape ecology (Farina 1998) and island biogeography (Mc Arthur and Wilson 1967, McLay and Hayward 1987). It is well established that the larger the holdfasts, the more invertebrates are generally supported (Smith and Simpson 2002, Anderson et al. 2005, Tuya et al. 2011). However, other attributes have received less research scrutiny, for example, if holdfast-associated invertebrates vary between different environments (Smith and Simpson 2002, Anderson et al. 2005), if the shape of the holdfast affects invertebrates, if the invertebrates only use the physical structure of the holdfast, if the holdfast structure needs to be biologically alive (Hauser et al. 2006) or if invertebrates vary between different kelp species (Tuya et al. 2011). Bull kelp holdfasts (and their invertebrate communities) are often lost from intertidal rocks due to storms (see Chapter 1, Santelices et al. 1980, Taylor and Schiel 2005, Wernberg and Connell 2008), anthropogenic stressors (Bustamante and Castilla 1990, Brosnan and Crumrine 1994, Benedetti-Cecchi et al. 2001) or natural disasters (see Chapter 3, Castilla 1988, Castilla and Oliva 1990, Castilla et al. 2010) where they sometimes are replaced

by other kelps, like the non-native Japanese kelp *Undaria pinnatifida* (see Chapter 3, Schiel et al. 2018). It is therefore important to test if new colonizing invasive kelp then provide similar ecological function as bull kelp.

I here address above outlined research gaps. More specifically I test if invertebrates associated with bull kelp holdfasts differ between

1. sites located along a latitudinal gradient in the South Island of New Zealand,
2. holdfast sizes,
3. holdfast morphologies (round vs. elongated shapes),
4. types (live vs. 3D printed abiotic models) and,
5. kelp species (*Durvillaea poha* vs. the fast-growing non-native kelp *Undaria pinnatifida*).

Research questions 1 and 2 were tested using holdfast collections whereas questions 3-5 were tested in a short-term factorial transplant experiment.

3.3 Methods

3.3.1 Holdfast collections.

A total of 24 holdfasts of different sizes were collected from 4 reefs situated along a 460 km latitudinal gradient; Kaikōura (42°25’29’’S 173°43’03’’E), Oaro (42°30’59’’S 173°30’22’’E), Pile Bay (43°37’05’’S 172°45’52’’E) and Moeraki (45°21’54’’S 170°51’48’’E). Note, however, that the Kaikōura holdfasts were collected from a reef that had been uplifted by 0.57 m (± 0.25 SE m) in a vertical zone dominated by green *Ulva* seaweed, 7 months after a large earthquake occurred (see Chapter 3 for details). These holdfasts were therefore stressed and would most likely die over the next 4-6 months (see Chapter 1 and 2). Randomly selected *Durvillaea poha* holdfasts were collected from intertidal bull kelp beds during low tide. Stipes were first cut off to remove blades, then holdfasts were detached from the rock with a chisel and quickly transferred to a plastic bag. Any invertebrates visible beneath the holdfast were also collected and added to the bag. Holdfasts were stored in a freezer until further processing.

3.3.2 Colonization of holdfast transplants

This experiment tested if holdfasts type, shape and species identity affect colonising invertebrates. I first created realistic mimics of *Durvillaea poha* and *Undaria pinnatifida*, using

a da Vinci 1.0 Desktop 3D printer to control shape traits (elongated vs. round) and size (by using the same amount of material per holdfast). This procedure removed potentially confounding factors between kelp species (for example, equal-sized bull kelp and *Undaria* will have different ages due to different growth rates). Approximately 100 digital photos were taken of a typical circular *U. pinnatifida* and *D. poha* holdfast covering the entire holdfast from different angles. The 3D models were created in "Autodesk Remake" and "Autodesk Meshmixer" was used for minor corrections and to 'elongate' the circular models. The final 3D models were printed in ABS plastic (Fig. 3.1). A total of 20 holdfasts were printed, each holdfast being composed of 2.5 m plastic filament (2 species × 2 shapes × 5 replicates). In October, 2017 5 circular and 5 elongated live holdfasts of similar length-width-depth dimensions to the printed plastic mimics, were collected of both *Undaria* and *Durvillaea*. The live holdfasts were rinsed in seawater, shaken vigorously and inspected closely for any small invertebrates that were thereafter removed. Mimics and live holdfasts were attached to a 1 m section of metal chain with cable ties and rubber bands. A small 5 x 4 cm piece of Astroturf was placed between the chain and the mimic to avoid breakage of the plastic mimics and facilitate rapid colonization of invertebrates. All holdfasts were separated by at least 30 cm on each chain. Chains were placed in shallow tide pools or in channels behind large rocks to reduce the risk of being lost due to wave actions; all in close proximity to live *D. poha* (a pilot experiment that attached mimics on an intertidal reef directly exposed to breaking waves had very high loss rate of mimics). Although these tide pools and channels are not the most typical bull kelp habitat, individual smaller bull kelp can occasionally be found there (pers. obs). Furthermore, this habitat still allows for valid tests of effects of holdfast shape, type and species identity. Transplanted holdfasts were collected 6 days later by cutting the rubber bands and cable ties and transferring Astroturf and holdfast to separate Ziploc bags. Holdfast and Astroturf samples were stored in a freezer until further processing.

3.3.3 Laboratory procedures

Holdfasts collected in the latitudinal survey were defrosted and vigorously rinsed in a 500 µm sieve. I used water, tweezers and brushes to extract invertebrates within small cavities of the holdfast. I did not break down the holdfast into small pieces to pry out the most hidden animals because all holdfasts were saved for future detailed 3D morphological analyses (but pilot sampling revealed that the majority of invertebrates were extracted with the methods used here). All animals retained on the sieve were stored in 70% ethanol. Animals were later counted

and identified under a stereo microscope (40× magnification) to operational taxonomic units (typical order for small inconspicuous organisms but genera or species for larger conspicuous organisms). I also recorded holdfast wet weight, two orthogonal holdfast diameters and stipe diameter (however, holdfast wet weight correlated strongly with holdfast and stipe diameters and, therefore, I only used wet weight in statistical analyses). Holdfasts collected from the experiment were processed in the same manner as outlined is 3.3.1 above, except that I used two sieve sizes to explore if most invertebrates were 'small' (250-500 µm) or 'large' (> 500 um).

3.3.4 Statistical analysis

Statistical analysis focused on five key invertebrate responses: taxonomic richness and the abundances of all invertebrates combined; crustaceans, gastropods and 'other invertebrates' (i.e., excluding crustaceans and gastropods). For the holdfast collections, 1-way ANOVA was used to test for differences between sites (fixed factor, where different sites represent different latitudes). Invertebrate data were, for these analyses, standardized to unit biomass (dividing richness or abundances by holdfast wet weight) and Log x+1 transformed to ensure variance homogeneity. Unstandardized invertebrate responses were thereafter related to holdfast wet weights with Spearman's rank correlation analyses. The experimental data were analysed with 3-factorial ANOVA (all factor were fixed), testing if invertebrate responses differed between holdfast species, types and shapes. This analysis was done on all the invertebrates combined from the two sieve classes and both the Astroturf and holdfast substrates, because this combination represented the spatially independent sampled unit with the highest invertebrate count. Richness (untransformed) and abundances (log x+1 transformed) all had homogenous variances (Levine's tests, $p > 0.09$ for all tests). Finally, I compared if more invertebrates were collected in the Astroturf or holdfast and if more invertebrates were 'small' or 'large'. This comparison was not analysed statistically in part because these factors were not related to my hypotheses about holdfasts attributes, in part because these data were not statistically independent.

3.4 Results

Holdfast collections. There were statistically significant effects of latitude on richness and abundance of 'other' invertebrates (Table 3.1, Fig. 3.2 and 3.3, $p < 0.001$), data were

standardized by holdfast wet weight), but no effect on all invertebrates, crustaceans or gastropods (see Fig. 3.2B and 3A-B, $p > 0.18$). Post hoc SNK tests showed more taxa and higher abundance of other taxa at the mid-latitudinal sites, Oaro and Pile Bay, compared to Kaikōura and Moeraki. Spearman rank correlations revealed significant relationships between all responses and holdfast wet weight; that is, there were significant effects for richness (Fig, 3.4A, $r = 0.577$, $p = 0.004$), all invertebrates (Fig. 3.4B, $r = 0.674$, $p < 0.001$), crustaceans (Fig. 3.5A, $r = 0.611$, $p = 0.002$), gastropod (Fig 3.5B, $r = 0.686$, $p < 0.001$), and other invertebrates (Fig. 3.5C, $r = 0.452$, $p = 0.030$).

3.4.1 Transplant experiment

Three of the responses, that is, richness ($p = 0.0008$, Table 3.2), crustacean ($p = 0.006$) and 'others' ($p < 0.0001$) were significantly affected only by holdfast type. More specifically, there were more taxa in live holdfasts than mimics (14.35 ± 0.88 vs. 10.10 ± 0.70, data variation refer to one standard error here and all other places). Similarly, I found more crustaceans (33.3 ± 6.1 vs. 11.7 ± 1.9) and more 'other invertebrates' (7.15 ± 0.88 vs. 3.20 ± 0.39) associated with live than mimic holdfasts. The total number of invertebrates was affected both by holdfast type ($p = 0.001$) and the Species × Type interaction ($p = 0.0431$, Table 3.2). This interaction reflected that although live holdfasts generally were colonized by more invertebrates than mimics, this effect was stronger for *Undaria* (live = 70.7 ± 12.48, mimics = 20.3 ± 3.71) than for *Durvillaea* (live = 33.2 ± 5.81, mimics = 22.3 ± 2.60). For gastropods, there were both significant Species × Type and Type × Shape interactions ($p = 0.0065$ and $p = 0.0053$, respectively, Table 3.2). The Species × Type interaction showed again that live *Undaria* holdfasts were colonized by more gastropods than mimics (16.5 ± 3.61 vs. 5.2 ± 0.99) whereas, by contrast, *Durvillaea* mimics supported slightly more gastropods than live holdfasts (7.6 ± 2.20 against a 6.6 ± 1.60). In addition, the Type × Shape interaction revealed that round mimic holdfasts were inhabited by more gastropods than elongated mimics (8.20 ± 2.34 vs. 4.60 ± 0.74) whereas elongated live holdfasts were inhabited by more gastropods than round live holdfasts (15.60 ± 3.73 vs. 7.52 ± 2.26). Finally, graphical analyses suggested that there were more small than large invertebrates (except for gastropods where large organisms were more common), and that more animals were collected in the Astroturf than the holdfast structures (Figs. 8-9).

3.5 Discussion

This study documented, as other holdfast studies have shown, a strong relationship between holdfast sizes and abundances of holdfast-associated invertebrates for *Durvillaea poha* from the South Island of New Zealand. Furthermore, I also showed that more invertebrates generally were associated with live than holdfast mimics and, for similar sized holdfasts, that the invasive kelp *Undaria* generally was a better habitat than *Durvillaea*.

3.5.1 Holdfast collections

Holdfasts were generally more diverse and inhabited by more invertebrates at the two mid-latitudinal sites. Other studies have also found different holdfast communities between geographical locations (Cancino and Santelices 1980, Christie et al. 2003, Anderson et al. 2005). For example, Smith and Simpson (2002) found, for *Durvillaea antarctica* holdfasts, higher abundance of annelids and nematodes, but lower abundances of crustaceans and gastropods, at wave exposed, compared to sheltered reefs. Smith and Simpson (2002) pointed out that these differences potentially were caused by co-variation in holdfast sizes and sediment contents. My site results could be explained by similar co-variation issues; the reported low diversity associated with the most southern site (Moeraki) included two very large holdfasts with relatively few invertebrates whereas the northern Kaikōura samples were 'stressed' because they were sampled 7 months after an earthquake-related uplift event (the holdfasts were intact and appeared healthy, but had damaged fronds) (Santelices et al. 1980, Castilla and Oliva 1990). Clearly, more holdfasts of similar sizes should be analysed from the study sites, as well as from un-impacted low latitudes reefs, to verify if the patterns observed here are consistent. However, the positive correlations with holdfast size were robust across animal responses (and sites) and thereby support previous holdfast studies that have found similar positive relationships (Sheppard et al. 1980, Smith 1996, Anderson et al. 2005, Tuya et al. 2011). This result also confirms standard island biogeography island patterns (Mc Arthur and Wilson 1967), and has been attributed to a combination of larger holdfasts (islands) having more habitat space, more habitat microclimates and micro-topographies and are older allowing more species more time to colonize these 'islands' (Sheppard et al. 1980, Ojeda and Santelices 1984, Anderson et al. 2005). Richness, in particular, tends not to increase linearly with holdfasts sizes, instead saturating because the regional species pools of invertebrates that can survive in this specialised habitat, can be limited (Ojeda and Santelices 1984, Anderson et al. 2005). Similarly, abundances can become increasingly inhibited by competition and predation

within the holdfasts as these structures grow larger (Ojeda and Santelices 1984, Anderson et al. 2005). It would be of particular interest to analyse more holdfasts from Kaikōura following the uplift along this coastline (Chapter 4). At the time of collection, only a few healthy *Durvillaea poha and D. antarctica* individuals remained, and reefs were colonized by green opportunistic *Ulva* species (Chapter 4). It was therefore surprising that the holdfast-associated invertebrate communities remained relatively intact, suggesting that these 'micro-landscape units' are closed systems that are resistant to external stressors (Edgar and Burton 2000). My results also highlight that the massive loss of bull kelp following the uplift (Chapter 4) will have dramatic negative impacts on the holdfasts associated invertebrates.

3.5.2 Transplant experiment

The transplant experiment showed that both biological and abiotic structures are rapidly colonized by a diverse community of small mobile invertebrates, as shown in other seaweed transplant experiments (Taylor 1998, Norderhaug et al. 2002, Roberts and Poore 2006, Aumack et al. 2011). The key result from the experiment was that the shape factors were of less importance compared to species identity and, in particular, if the holdfast was alive or a mimic, where more organisms were found for the live than mimic holdfasts, and, to a lesser extent, for *Undaria* compared to *Durvillaea*. I am not aware of other kelp holdfasts studies that have tested for shape effects, but larger landscape studies have often concluded that habitat configuration can affect biodiversity (Fahrig 2003, Paracuellos and Tellería 2004). Perhaps, I found slightly more invertebrates in the elongated than round holdfasts (but only for live holdfasts) because they have more microstructures and a larger perimeter and therefore larger 'edge effects' and more 'ecotones' (Fahrig 2003). The finding that live holdfasts supported higher biodiversity than mimics can partly be explained because live holdfasts provided both a structural habitat and also a trophic resource for mesograzers, as documented from other marine habitats (Bologna and Heck 1999, Koivisto and Westerbom 2010, Macreadie et al. 2014). More importantly, more animals were probably found in live holdfasts because the live holdfasts had more structural variability (the mimics were all completely similar) and finer-scale microstructures (holdfasts were printed with a minimal thickness of 4 mm to avoid breakage). Finally, I found higher biodiversity associated with the invasive kelp *Undaria* compared to *Durvillaea*, but only for live holdfasts. This may reflect that live *Undaria* holdfasts are morphologically more complex containing more small interstitial spaces than live bull kelp

holdfasts (Fig. 3.1, but this was less pronounced for the mimics that were printed in thicker forms), as suggested for other kelp species (Tuya et al. 2011).

3.5.3 Ecological implications and conclusion

This study provided baseline data on biodiversity associated with bull kelp and invasive *Undaria* holdfasts. These results are important to better understand ecosystem-wide impacts following local (Chapter 2) and regional (Chapter 4) disturbances to bull kelp forests, as well as better understand long distance dispersal of mobile animals through 'rafting' on dislodged bull kelp (Blight and Thompson 2008, Gutow et al. 2009, Collins et al. 2010, Fraser et al. 2011, Haye et al. 2012, Tala et al. 2013, Cumming et al. 2014, Gutow et al. 2015). It should also be noted that although I found more invertebrates with *Undaria* than bull kelp for similar-sized holdfasts, the *Undaria* habitat is much more ephemeral and generally much smaller as *Undaria* holdfasts persist for less than a year compared to up to 10 years for bull kelp holdfasts (Hay 1977, Schiel and Thompson 2012, South et al. 2016). Finally, I conclude that bull kelp holdfasts provide an abundant and robust habitat for small mobile animals; when these structures are lost through natural disturbances or anthropogenic stressors, so is the diverse fauna that inhabit these biological structures.

Table 3.1 Holdfast survey. Anova testing for effects of 4 regions situated along a latitudinal gradient, for richness and abundances of all animals pooled, crustaceans, gastropods and remaining animals (other). Animal data were standardized by holdfast size (gWW) and log (x+1) transformed to ensure variance homogeneity. Significant results ($p < 0.05$) are in bold.

Variable	**Factor**	**SS**	**DF**	**F**	**P**
Richness	Latitude	2.679	3	13.945	**0.000**
	Error	1.217	19		
All	Latitude	0.568	3	1.769	0.187
	Error	2.033	19		
Crustaceans	Latitude	0.642	3	1.196	0.338
	Error	3.397	19		
Gastropods	Latitude	0.518	3	0.590	0.629
	Error	5.555	19		
Others	Latitude	5.133	3	13.700	**0.000**
	Error	2.373	19		

Table 3.2 Factorial ANOVA for: Richness, all invertebrates, crustaceans. gastropod, and 'other' invertebrates. Abundance data were log x+1 transformed to ensure variance homogeneity. Random factors for all of them were: species (spe), type, shape, spe × type, spe × shape, type × shape, spe × type × shape. Significant results ($p < 0.05$) are in bold.

Test	**Factor**	**SS**	**Df**	**F**	**p**
Richness	Species (Spe)	1.225	1	0.094	0.7613
	Type	180.625	1	13.841	**0.0008**
	Shape	11.025	1	0.845	0.3649
	Spe × Type	13.225	1	1.013	0.3216
	Spe × Shape	0.625	1	0.048	0.8282
	Type × Shape	42.025	1	3.220	0.0822
	Spe × Type × Shape	0.625	1	0.014	0.8282
	Error	417.600	32		
All invertebrates	Species (Spe)	0.082	1	0.943	0.3389
	Type	1.116	1	12.881	**0.0011**
	Shape	0.053	1	0.613	0.4395
	Spe × Type	0.385	1	4.438	**0.0431**
	Spe × Shape	0.011	1	0.122	0.7289
	Type × Shape	0.187	1	2.162	0.1512
	Spe × Type × Shape	0.001	1	0.014	0.9058
	Error	2.773	32		
Crustaceans	Species (Spe)	0.047	1	0.284	0.5977
	Type	1.454	1	8.716	**0.0059**
	Shape	0.223	1	1.337	0.2562
	Spe × Type	0.358	1	2.143	0.1530
	Spe × Shape	0.044	1	0.265	0.6100
	Type × Shape	0.038	1	0.231	0.6343
	Spe × Type × Shape	0.001	1	0.005	0.9444
	Error	5.340	32		

Figure 3.1 Various holdfast photos. A = *Durvillaea* holdfast, B = *Undaria* holdfasts, C = Holdfast cavity with limpets, D, E = live and 3D printed mimic attached to Astroturf and chains, F = Holdfast cavity with two protruding arms of a large seastar.

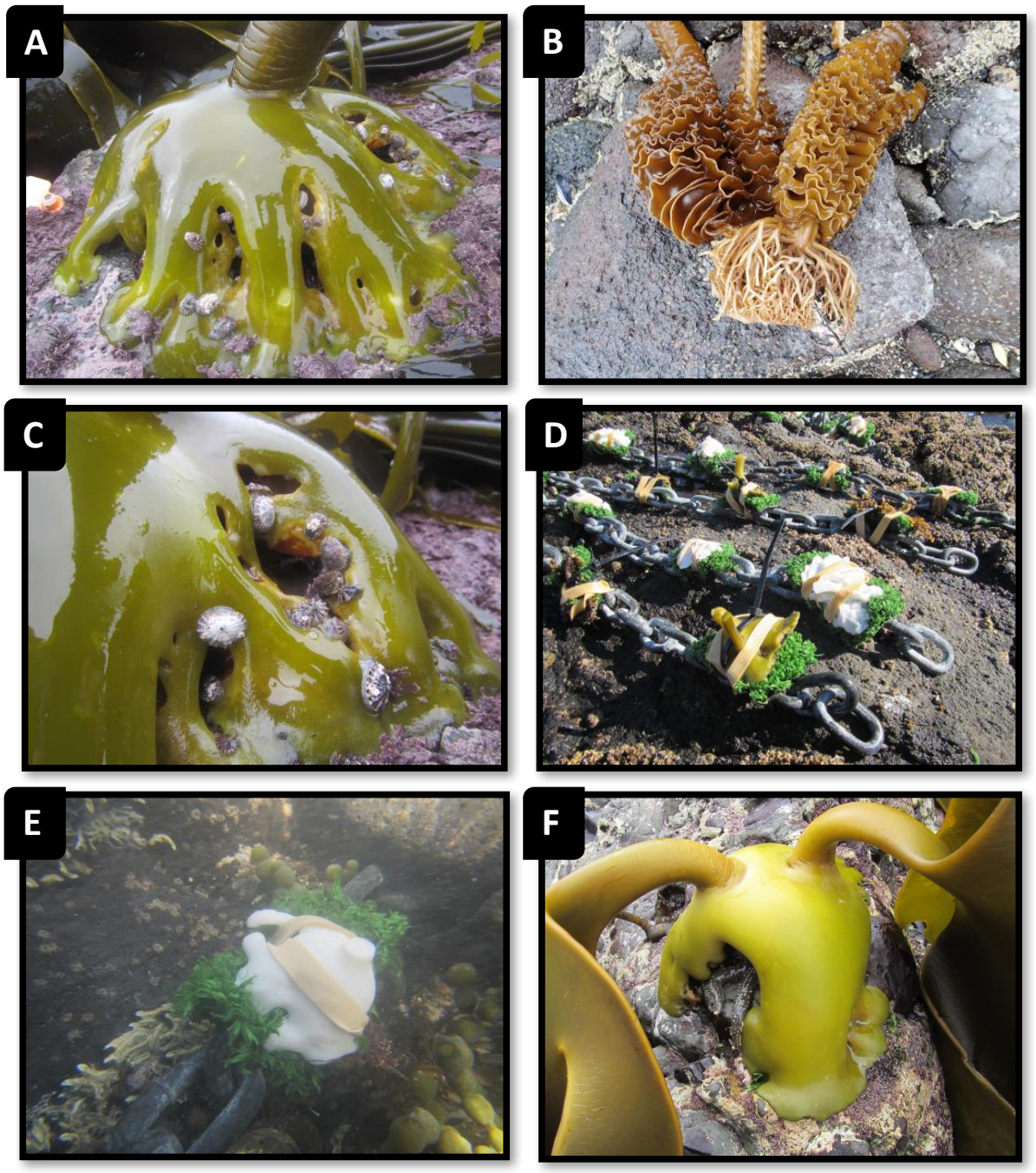


Figure 3.2 Holdfasts collections. Taxonomic richness (A) and abundances of all invertebrates (B) for 4 sites positioned along a latitudinal gradient. Error bars are SE, n from left to right = 6, 4, 5, 8.

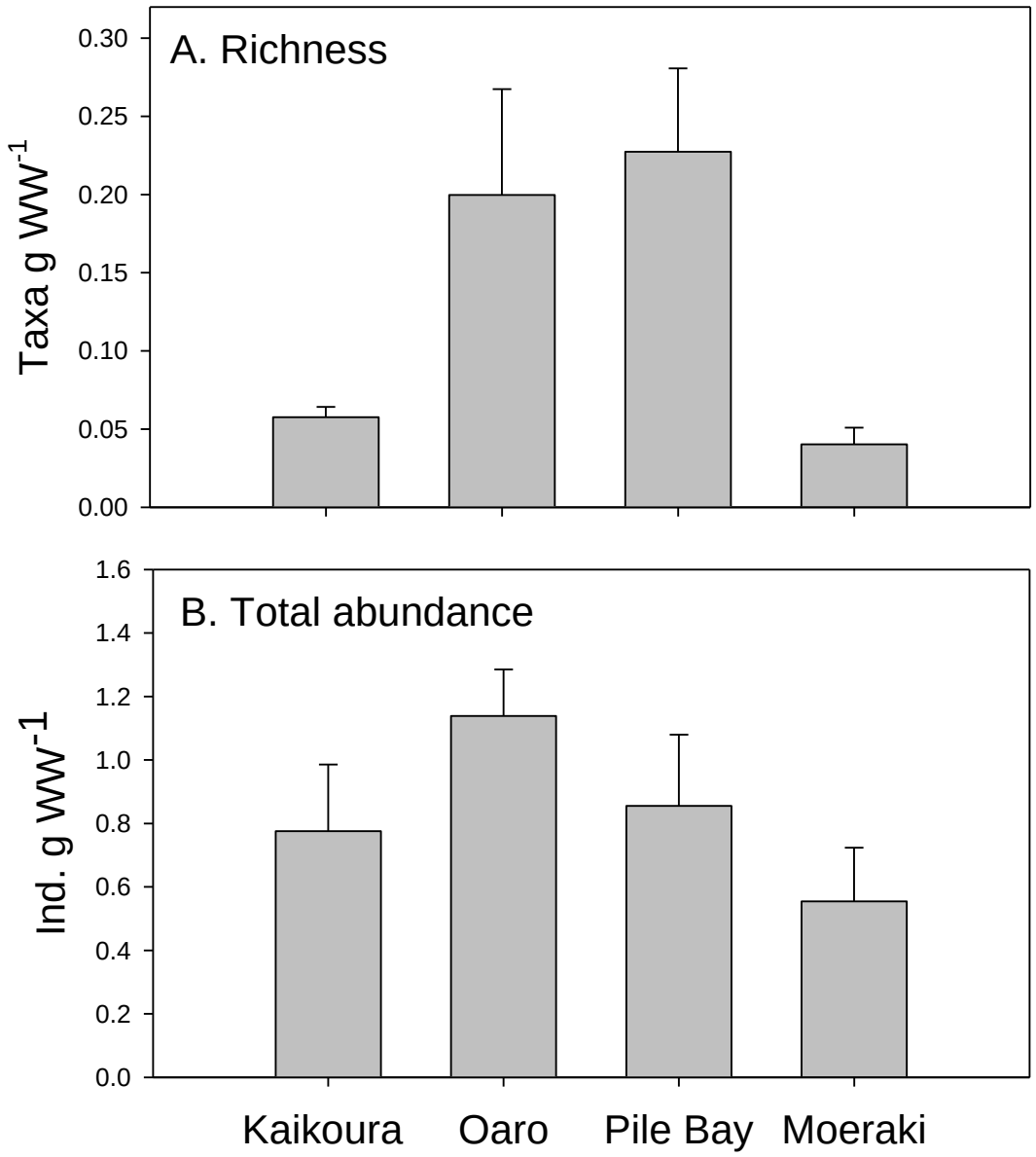


Table 3.3 Holdfasts collections. Abundance of crustaceans (A), gastropods (B) and ‘other’ invertebrates (C) for 4 sites positioned along a latitudinal gradient. Error bars are SE, n from left to right = 6, 4, 5, 8.

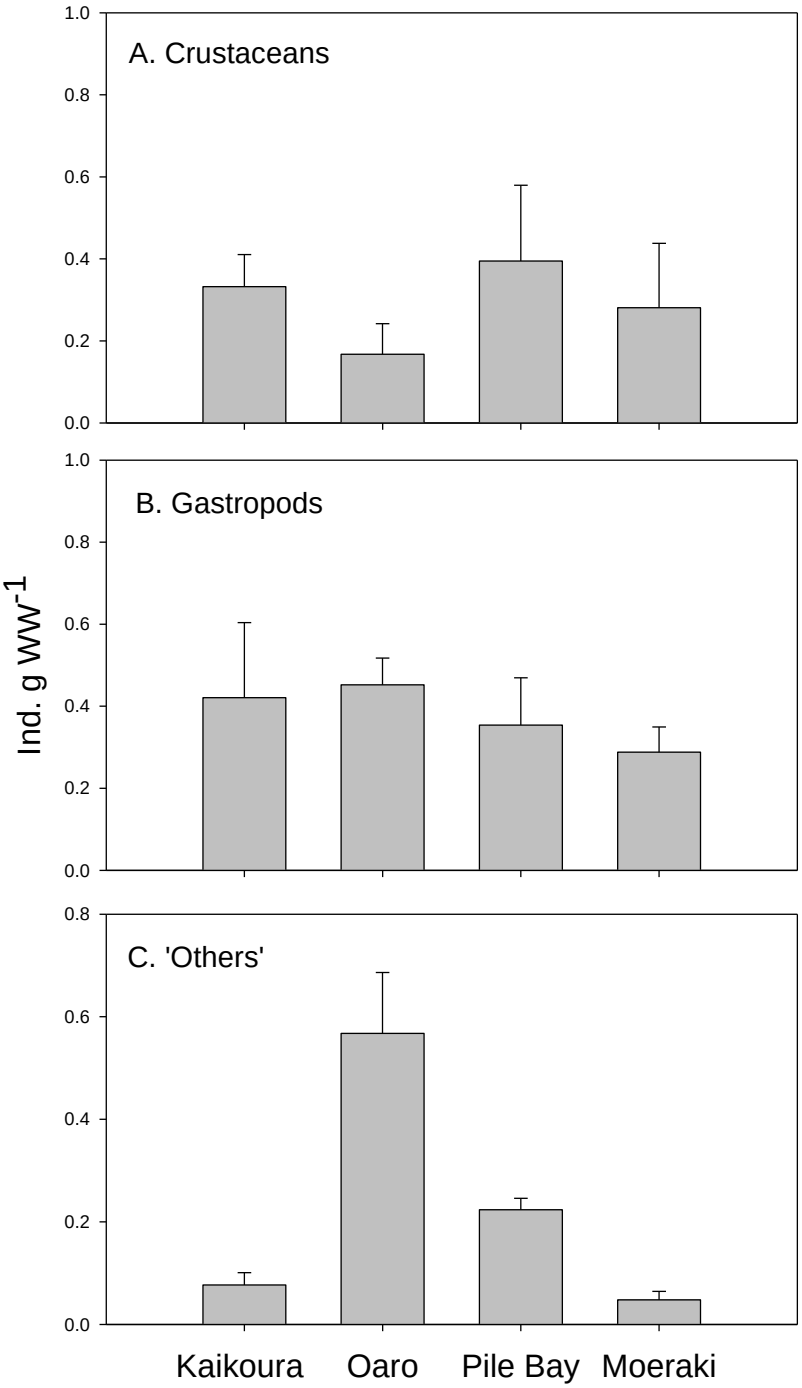


Table 3.4 Holdfasts collections. Holdfast size (g WW) vs. taxonomic richness (A) and total number of invertebrates (B). Diamond = Moeraki, Circle = Oaro, Square = Pile Bay, and Downward triangle = Kaikōura. p-values and r correspond to Spearman ranks correlations.

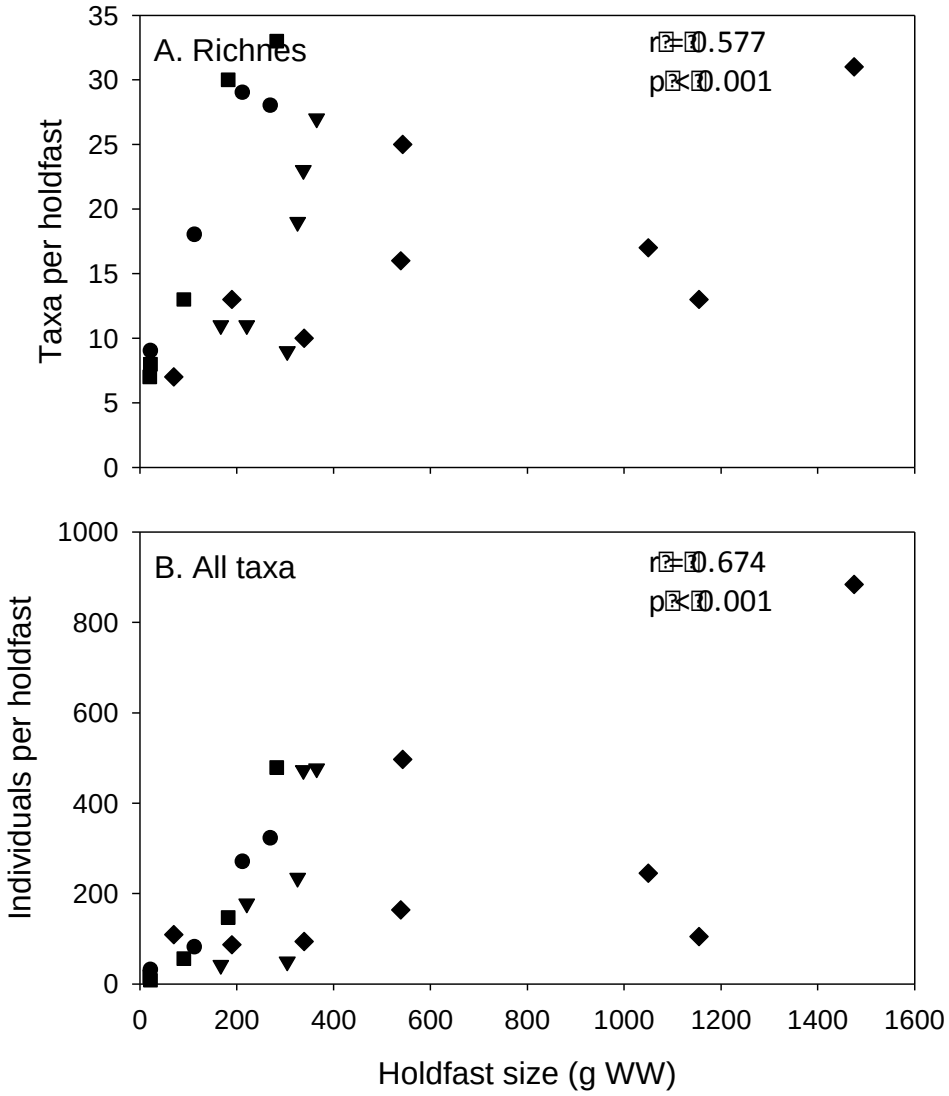


Table 3.5 Holdfasts collections. Holdfast size (g WW) vs. abundance of crustaceans (A) gastropods (B) and 'other' invertebrates (C). Diamond = Moeraki, Circle = Oaro, Square = Pile Bay, and Downward triangle = Kaikōura. p-values and r correspond to Spearman ranks correlations.

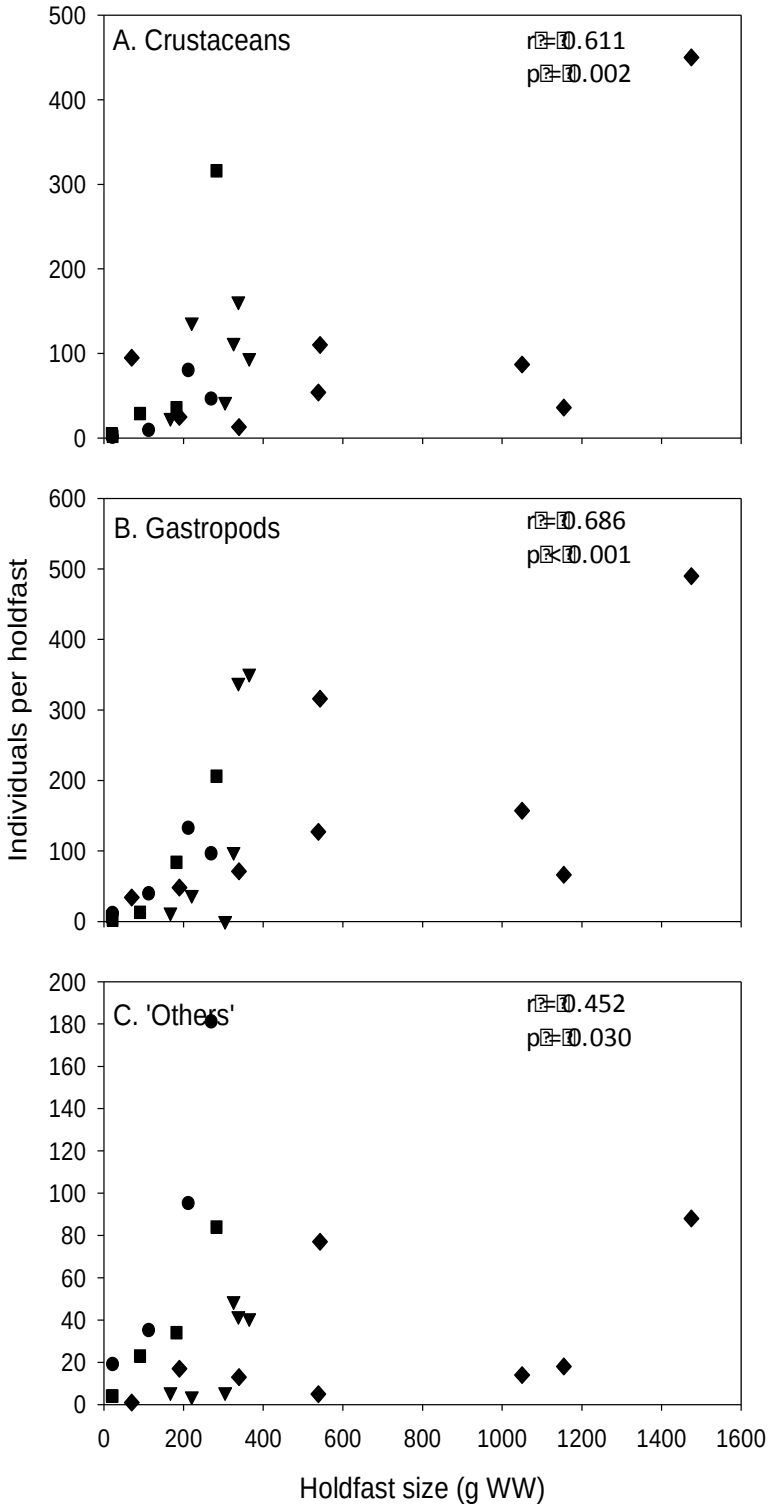


Table 3.6 Experiment testing for effect of species identity, type and shape on kelp holdfast invertebrate communities, including taxonomic richness (A) and total abundance (B). Legend: D = *Durvillaea* species, U = *Undaria* species, L = Live type (and grey bars), M = Mimic type (and white bars), E = Elongated shape, R = Round shape. Error bars are SE, n = 5.

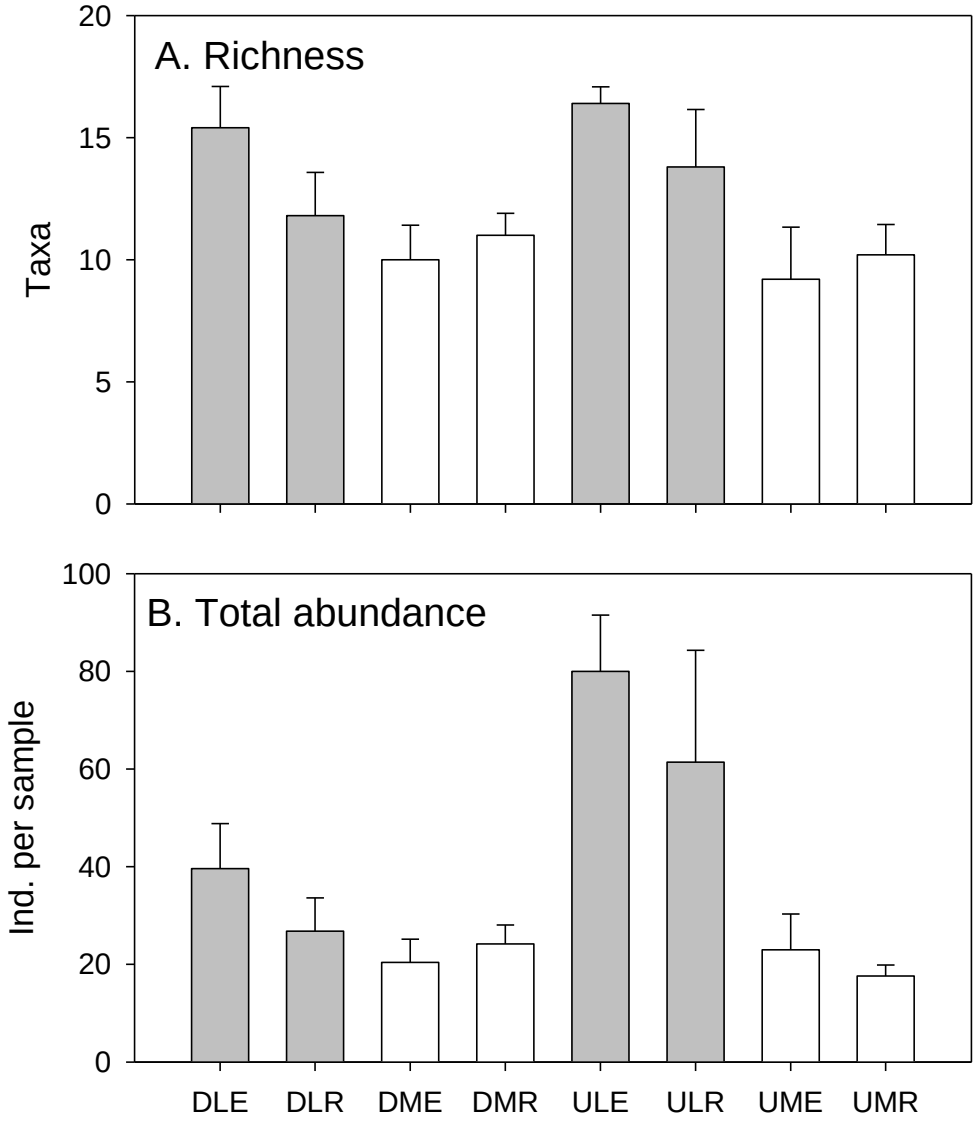


Table 3.7 Experiment testing for effect of species identity, type and shape on kelp holdfast invertebrate communities; here abundances of crustaceans (A), gastropods (B) and ‘other invertebrates (C). Legend: D = *Durvillaea* species, U = *Undaria* species, L = Live type (and grey bars), M = Mimic type (and white bars), E = Elongated shape, R = Round shape. Error bars are SE, n = 5.

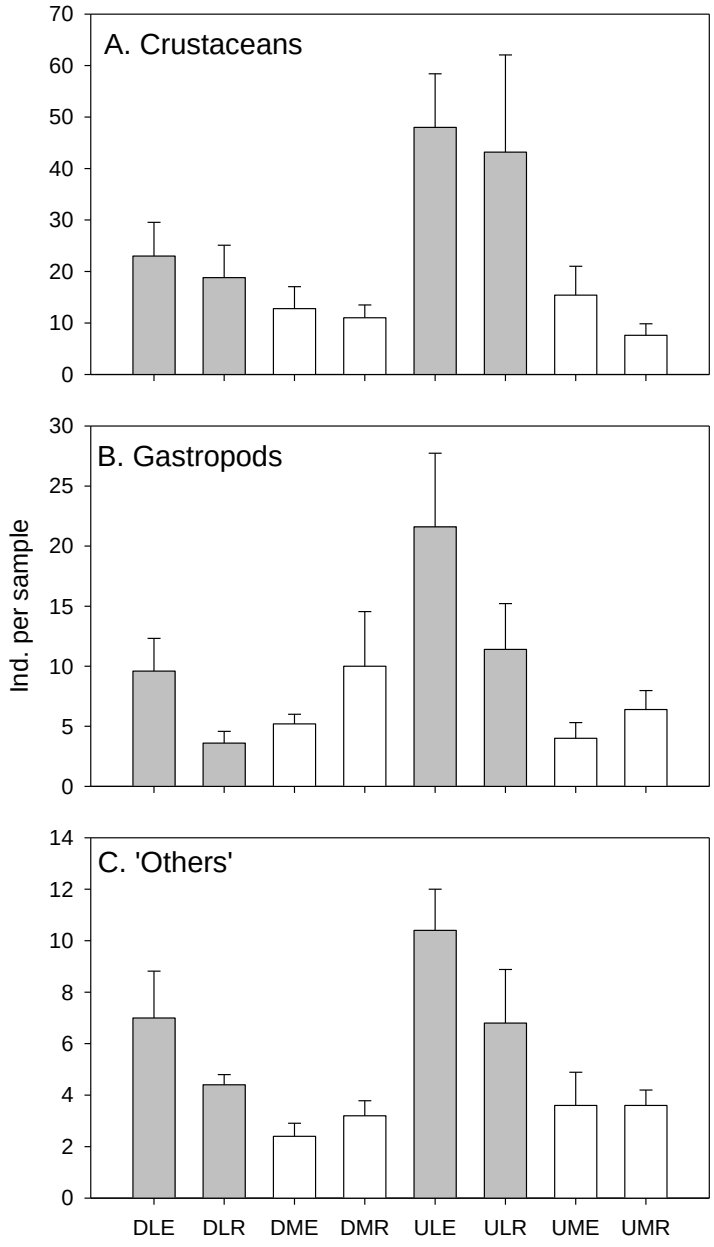


Table 3.8 Experiment testing for effect of species identity, type and shape on kelp holdfast invertebrate communities. Data here were pooled across the three test factors and instead shown for richness (A) and total abundance (B) of small (250-500 um) and large (>500 um) invertebrates collected either in the basal Astroturf substrate (Turf) or the holdfast (HF) (see Methods for details). Error bars are SE, n = 40.

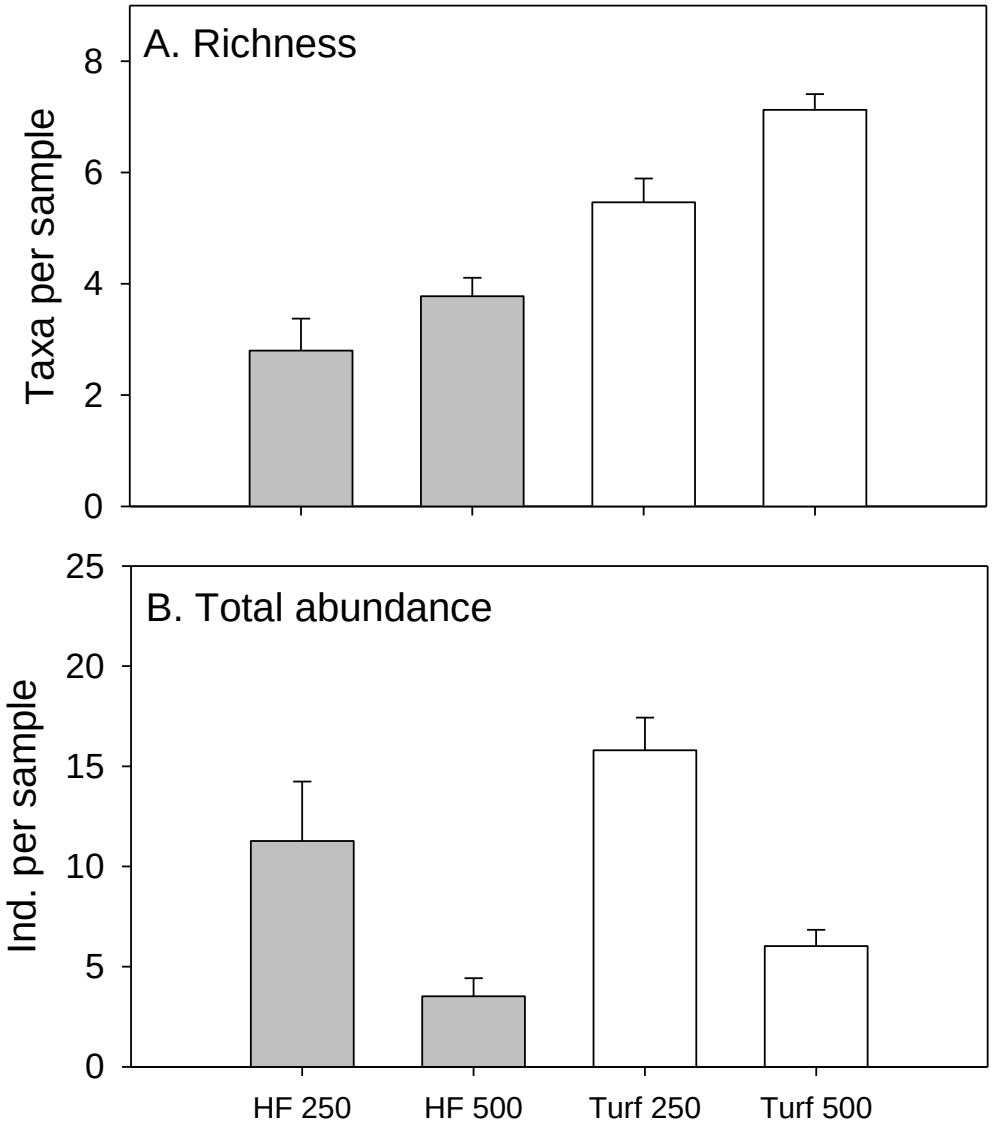
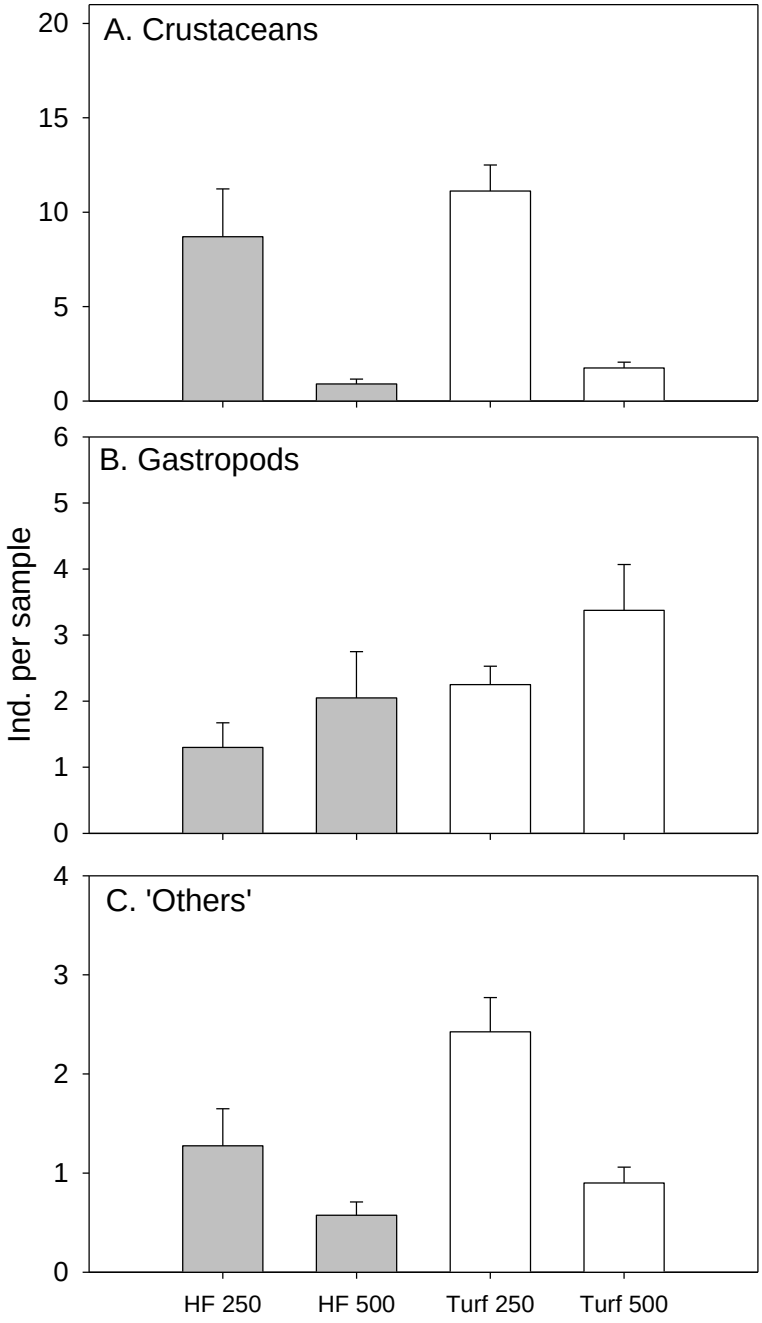


Table 3.9 Experiment testing for effect of species identity, type and shape on kelp holdfast invertebrate communities. Data here were pooled across the three test factors and instead shown for abundances of crustaceans (A), gastropods (B) or 'other' invertebrates (C) of small (250-500 μm) and large (>500 μm) invertebrates collected either in the basal Astroturf substrate (Turf) or the holdfast (HF) (see Methods for details). Error bars are SE, N = 40.



Chapter 4:

Loss and potential recovery of bull kelp after an earthquake and reef uplift

4.1 Abstract

On November 14th, 2016, a 7.8 M_w earthquake hit the north-eastern part of New Zealand's South Island resulting in vertical deformation of reefs along a 130 km coastline with uplifts ranging from -0.2 m to 6 m. Strong impacts were visible immediately on marine communities, in particular on dominant intertidal bull kelp (*Durvillaea* spp.). Bull kelp are productive 'foundation species' that through large blades and holdfast structures have a strong effect on local community structure and ecosystem functioning; it is therefore important to have baseline information of how much kelp was lost along this coastline. The aim of this study was to provide baseline data on bull kelp loss, compare data to an un-impacted bull kelp bed, relate degree of uplift with bull kelp loss, and examine if bull kelp would recover from uplifted areas where fronds initially died back leaving only holdfasts and stipes. I surveyed 16 reefs from Oaro to Kaikōura peninsula with uplifts ranging from -0.2 to 2.2 m 3-4 months after the earthquake. Randomly positioned 0.5 × 0.5 m quadrats were sampled by taking photos perpendicular to the substrate at reef sections with clear traces of dense bull kelp holdfasts, i.e. where there were healthy bull kelp beds prior to the earthquake. These reef sections were then subdivided into (1) a higher zone turned white due to decaying calcifying encrusting alga, (2) a middle-zone turned green due to colonization of opportunistic *Ulva* spp. seaweed, and (3) a lower red zone where understory red encrusting alga remained intact. In total, 1658 quadrats were analysed for (a) percent cover and (b) density of 'holdfast scars' (circular areas of newly exposed fresh rock), (c) stipes without blades, (d) stipes with blades, and (e) percent cover of holdfasts. Also, in order to examine persistence of holdfasts for each reef, 20 stipes in the lower intertidal zone were double-tagged. I found, for uplifted reefs, increases toward the white zone for cover and number of holdfast scars, decreases toward the new tidal upper zone for stipes with blades and cover of attached holdfasts, and that stipes without blades had highest densities in the mid-green zone. By contrast, there was no similar white zone at the single reef experiencing submergence (Oaro) and this reef had much fewer holdfast scars and stipes without blades. Finally, tagged stipes from the green zone were lost from uplifted reefs but survived at Oaro, ca. 8 months after tagging, suggesting that most kelp in the green zone would eventually die. Overall, my survey documented extensive loss of bull kelp along ca. 15 km coastline, a result that likely can be extrapolated to other areas of the coast that have experienced similar or more severe uplifts. These losses of bull kelp are likely to have long-lasting and wide-ranging ecological effects. It will be of great importance to follow these beds

in future years to test if similar sized bull kelp forest will establish by downward shifts or if remnant surviving beds will remain small.

4.2 Introduction

Marine wave-exposed intertidal rocky shores are some of the most stressful biological habitats on earth. In this zone, organisms experience daily changes in desiccation, temperature, light and wave battering. Some marine organisms are well-adapted to these conditions, typically resulting in species-specific zonation patterns that often are generally determined upwards by physiological tolerances (in particular desiccation tolerance) and downward by biological interactions, like competition and consumption (Connell 1961, 1975, Lubchenco 1980, Connell 1983, McQuaid and Branch 1985, Underwood 1998, Chappuis et al. 2014).

Temperate rocky shores are also characterized by many other types of stressors and disturbances ranging widely in spatio-temporal scales and return times, including storm waves (Ebeling et al. 1985, Seymour et al. 1989, Wernberg and Connell 2008), local anthropogenic stressors, like nutrient and sediment pollution and invasions by non-native species (Brosnan and Crumrine 1994, Benedetti-Cecchi et al. 2001, Castilla et al. 2007, Campbell et al. 2014), large climatic events like the El Niño–Southern Oscillation (Schiel and Foster 2015), slower climate changes (Glynn 1988, Underwood 1998, 1999, Thompson et al. 2002), heat waves (Smale and Wernberg 2013, Wernberg et al. 2013), or even tectonic activities like formation of volcanos (Hauksson 2000, Jónsson and Gunnarsson 2000) or vertical displacement following earthquakes (Castilla and Oliva 1990, Castilla et al. 2010). Tectonic disturbances have been relatively little studied, probably because they are rare events, mainly occurring along plate subduction zones. However, when and where vertical rock movement occurs around the intertidal coastal zone, impacts can be severe and long lasting (Lebednik 1973, Castilla 1988). Coastal uplift resulting from earthquakes has been studied both in geological (Barrientos et al. 1992, Clark et al. 2017) and ecological (Bustamante and Castilla 1990, Castilla et al. 2010) contexts. In the latter studies dramatic changes in zonation patterns of intertidal organisms have been recorded, especially in the first year after the earthquake (Castilla and Oliva 1990, Castilla et al. 2010). The main effects described in past studies were (a) widespread loss of individuals of many different species, (b) alteration of vertical zonation patterns, (c) increase in patchiness, (d) opening of new space, and (e) rapid colonization of ephemeral species (Bustamante and Castilla 1990, Castilla et al. 2010). Indeed, these biological

changes to zonation patterns have been used to estimate vertical displacement at locations with poor vertical benchmark data (Bodin and Klinger 1986, Castilla et al. 2010).

On temperate coastal rocky shores, canopy forming kelps and large fucoids often dominate the biomass, creating habitat for many other species and affecting ecosystem functions, like productivity, sediment accumulations, wave attenuation and light levels (Dayton 1985, Smith and Bayliss-Smith 1998, Anderson et al. 2005, Taylor and Schiel 2005, Wernberg et al. 2005, Irving and Connell 2006). Previous studies, that have quantified impacts from earthquake related uplifts in Chile, have documented dramatic effects on foundation species, sometimes recording 100% mortality in specific elevation zones for *Macrocystis pyrifera*, *Lessonia nigrescens* and *Durvillaea antarctica* (Castilla 1988, Castilla et al. 2010), but with less mortality in the lower zones and with rapid recruitment in the following years. However, there are few studies that have recorded earthquake-related impacts on intertidal canopy forming seaweed outside of South America.

Here I investigate earthquake-related effects on bull kelps (mainly *Durvillaea poha*, *D. antarctica* and some *D. villana*) following the November 14th 7.8 M_w Kaikōura earthquake on the South Island of New Zealand. Sixteen reefs were surveyed, situated between the Kaikōura peninsula and the village of Oaro, a coastline of around 20 km (of which around 15 km are of rocky shore) characterized by uplifts ranging from 0.4 to 2.2 m at 15 of these reefs, and submergence by 0.2 m at Oaro (the 'control' reef, see Table 4.1 for details). A few patches of reefs that were not affected by the earthquake were also found along this coastline, but road work and instability of adjacent cliffs made those sites inaccessible. More specifically, the aim of this study was to provide baseline data on bull kelp loss along the coastline, compare data between uplifted reefs and Oaro, relate bull kelp loss to the degree of uplift, and examine if bull kelp that lost blades relatively soon after the earthquake would recover.

4.3 Methods

To quantify impacts on bull kelp I surveyed 16 reefs along ca. 15 km coastline from Oaro (42°30'59''S 173°30'22''E) to the Kaikōura Peninsula (42°25'29''S 173°43'03''E). These reefs were studied because (a) many parts of this shoreline were dominated by bull kelp prior to the earthquake (Schiel and Hickford 2001), (b) reefs were characterized by a gradient in uplift from -0.2 m at Oaro to 2.2 m (see Table 4.1), (c) these reefs have great cultural, recreational, and economic value to the local community and (d) reef access was allowed and safe (other reef sections were closed for roadwork and/or had unstable adjacent hills). I only

surveyed reef sections that clearly were dominated by bull kelp prior to the earthquake (because there was clear evidence of bull kelp holdfasts, see Fig. 4.1). These reef sections were then divided into three elevation zones that were easy to separate visually; (a) a higher zone that turned 'white' because encrusting calcifying organisms had died, (b) a middle zone that had turned 'green' because it was invaded by opportunistic green alga *Ulva* spp., and (c) a lower 'red' zone where the understory was dominated by red encrusting alga (Fig. 4.1) These zones therefore do not correspond to classic 'high', 'mid' and 'low' intertidal zones, but represents pre-earthquake low-to-shallow subtidal zones. The red zone was only partially emergent on a few low spring tides so fewer samples were collected here (see Table 4.1). The main focus of this survey was on documenting losses of the intertidal bull kelp, *D. poha* and *D. antarctica*, and these species were much less common in this red zone that previously was subtidal and dominated by *D. willana.*

Reefs were sampled during low tide, 3-4 months after the earthquake when access was logistically possible and safe. At each reef, I took photos of randomly positioned 0.5 × 0.5 m quadrats covering the three zones of the post-earthquake configuration (see Fig. 4.1 for examples and Table 4.1 for details of sample sizes and reef characteristics). For each quadrat, within each of the three elevation zones, I quantified (1) number of stipes with blades, (2) number of stipes without blades, (3) percent cover of holdfasts (considering both holdfasts with or without blades) (4) number of holdfast scars, and percent cover of (5) holdfast scars. I counted stipes instead of holdfasts, because each stipe represents an individual genotype – whereas multiple holdfasts often coalesce and therefore represent multiple individuals (e.g., see Fig. 4.1E, where many stipes can be seen arising from a single holdfast). Holdfast 'scars' were defined as near-circular reef sections of similar sizes to holdfasts, exposing new bare reef without any sessile organisms. These scars were morphologically similar to the reef scars left after I manually removed holdfasts (see Chapter 1 and 2), but I cannot completely rule out that other organisms or processes created some of these clean round(ish) rock structures.

I also double-tagged 20 stipes (including both adult and juvenile kelp) on 9 of the uplifted reefs and Oaro, mostly in the green mid-zone where many fronds were lost but stipes remained, to investigate if these individuals would recover from the uplift stress. These reefs were revisited in November 2017, when I counted surviving individuals.

4.3.1 Statistical analysis

All bull kelp responses, that is, percent cover and density of scars, percent cover of holdfasts, and density of stipes with and without blades, had strong heteroscedasticity (Levine's tests, $P < 0.0001$) and could not be transformed to variance homogeneity. I therefore used pairwise non-parametric Mann-Whitney tests to test for differences in bull kelp responses between un-impacted Oaro vs. the impacted reefs and between the three elevation zones. First, I pooled data across zones to test if the uplifted reef responses differed from Oaro. For these tests data from the white zone was excluded because no white zone was observed at Oaro. Second, I pooled data across the uplifted reefs (i.e. without Oaro data) to test if the three elevation zones had different bull kelp responses. Finally, a series of correlation (Spearman ranks) analyses were used to investigate if mean kelp responses per reef varied with vertical reef displacement within an elevation zone (ranging from -0.2 to 2.2). Although the three elevation zones 'incorporate' the biological responses associated with degree of uplift (e.g., the white zone was likely to be more extensive vertically on reefs with high than low uplift) it is still possible and of interest to test if severity of impact varied systematically (within a zone) with degree of uplift.

4.4 Results

There were significant differences in kelp responses between Oaro and uplifted reefs in the red zone, for all responses except 'stipe with blades' (Fig. 4.2). However, in the green zone only 'stipe without blades' and 'holdfast percentage of cover' were significantly different between Oaro and the uplifted reefs (Fig. 4.2). More specifically, densities of stipes without blades were lower at uplifted reefs compared to Oaro in both the red (0.07 ± 0.02 vs. 1.25 ± 0.15, data variability refer here and everywhere to 1 standard error) and green (0.125 ± 0.12 vs. 2.16 ± 0.07) zone. Similarly, percent cover of holdfast was lower at uplifted reefs compared to Oaro, for both the green (4.25 ± 2.89 vs. 13.3 ± 0.42) and red (11.96 ± 0.65 vs. 18.3 ± 0.91) zone. Furthermore, in the red zone, both densities of holdfast scars (0.49 ± 0.07 vs. 0.20 ± 0.04) and percent cover of scars (2.97 ± 0.47 vs. 1.05 ± 0.25) were higher at the uplifted reefs compared to Oaro.

For the uplifted reefs only, most kelp responses were significantly different between different elevation zones (Table 4.3). I found significant decreases, from the red to the green to the white zone, in percent cover (Fig. 4.2A) and density (Fig. 4.2B) of holdfast scars, and significant increases in percent cover of holdfasts (Fig. 4.2E). More specifically, percent cover of holdfast

scars decreased from 9.38 (± 0.49) to 2.97 (± 0.47), density of holdfast scars decreased from 2.08 (± 0.11) to 0.49 (± 0.07) whereas percent cover of remaining holdfasts increased from 7.77 (± 0.51) to 18.33 (± 0.92), from the white to the red elevation zone. For stipes without blades there were significantly highest densities in the green zone (2.17 ± 0.07; Fig. 4.2C) with similar lower densities between the white and red zones (1.29 ± 0.12). Finally, I found that densities of stipe with blades where higher in the red zone compared to the white and green zones (Fig. 4.2D, 4.41 ± 0.34 vs. 0.25 ± 0.05).

Although there were strong significant effects in kelp responses between uplifted elevation zones and between uplifted reefs and Oaro (Fig. 4.2), only one out of 15 correlations between degree of uplift and kelp response (per zone) was significant (Table 4.4, Fig. 4.3-4.7). This single significant result showed a negative relationship between uplift and density of stipes with blades within the green elevation zone (Fig 6B, but note that mean cover values where very low (<1.5%) suggesting relatively low ecological relevance of this test).

Finally, all tagged stipes from the 9 uplifted reefs were lost, whereas 19 out of 20 tagged stipes were found again at Oaro.

4.5 Discussion

This survey confirmed that the uplift following the 14th November 2016 Kaikōura earthquake caused widespread mortality to intertidal bull kelp. Two main forms of loss were observed 3-4 month after vertical uplifts that ranged from 0.4 to 2.2 m: loss of blades and loss of entire holdfasts. The intertidal species *D. poha* and *D. antarctica* were most severely affected whereas subtidal *D. willana*, appeared to be less affected (pers. obs.).

4.5.1 Disturbances to kelp and uplift

Kelp die naturally due to old age, diseases, storms and through grazing, but also increasingly due to overgrazing by expanding urchin fronts, increased competition from turf-alga, warming, eutrophication, enhanced sedimentation, and invasive species (Estes and Duggins 1995, Graham 2004, Connell and Russell 2010, Wernberg et al. 2016). Most of these stressors are, however, localized events (but see Wernberg et al. (2013) for a large scale regional extinction event). I here add to this mixture of local stressors, showing region-wide impacts following an earthquake and reef uplift, with dramatic losses in a white and green elevation zones with only few surviving stipes with attached blades (see Fig. 4.2D, stipes without blades did not survive,

cf. the tagging experiment and results from manipulated stipe cuttings in chapter 1). These types of large scale die-off events are considered to be rare, are rarely observed and therefore rarely studied. However, similar events in Chile (Castilla 1988, Bustamante and Castilla 1990, Castilla et al. 2010) and geological records of past uplifts and seismic activity (Barrell 2015) suggest that these events may be relatively common on longer time scales (particular along the world's coastal plate subduction zones), and therefore, perhaps, have an overlooked importance in explaining present day species distribution patterns. For example, Castilla (1988) and Castilla et al. (2010) described extensive mortality of intertidal kelp and other communities after a large 1985 earthquake in Chile, with patterns very similar to what was observed here. More specifically, the uplifted high zone in Chile had highest kelp mortality, like the white zone described here. Similarly, for the mid zone, Castilla (1988) first reported changes to the colours of kelp holdfast, follow by slow decay and, ca. one year after the earthquake, death and dislodgment. The loss of blades reported here for the green mid-zone appear to follow the pattern observed in Chile. Finally, the lower kelp zone was described only to experience minor changes as appears to be the case for the red zone along the Kaikōura coastline (Castilla 1988, Castilla and Oliva 1990, Castilla et al. 2010).

Although I found strong impacts of uplift, there were no clear correlations between impact and degree of uplift. The key reason for this is that these biologically defined zones most likely already have incorporated biological effects associated with degree of uplift, for example, if the white zone is vertically larger at reefs with more severe uplifts. I did not have access to high resolution topographic GPS equipment (and all past vertical baseline fix-point had been destroyed) so it was, unfortunately, not possible to estimate the vertical band of the white and green zones. In addition, smaller scale topographic anomalies (for example, with small scale low areas where bull kelp survive in pockets), uncertainties associated with the reported uplift, and the relatively small differences between ranges of uplift, further reduces the likelihood of finding relationship between degree of uplift and impact on bull kelp (by contrast, where maximum uplift occurred along the entire impacted coastline, with 6 m uplift at Waipapa bay, 100% of the uplifted kelp, of course, died; Schiel DR, unpubl. data).

4.5.2 Replacement of kelp with early colonizing species and implications

As shown experimentally in Chapter 1, loss of bull kelp blades, stipes and holdfasts can lead to colonization of opportunistic seaweed, following competitive release from blade whiplash and shading. My survey here was designed to document large scale loss of bull kelp, not new

colonization by turf forming alga. However, it is most likely, from my analysis of healthy bull kelp reefs in Chapter 1 and observations from Oaro with unaffected bull kelp, that the prolific *Ulva* beds along the entire Kaikōura coastline within the elevation zone previously occupied by bull kelp (Fig. 4.1) are a result of the uplift and the loss of bull kelp blades. Indeed, my quadrat survey showed that in the green zone, *Ulva* covered, on average across the 15 uplifted reefs, 68% of the substratum, and that this zone in many cases was many meters wide (Fig. 4.1, pers. observation). Similar wide zones with *Ulva* dominance have rarely been observed on intertidal rocky shores in New Zealand (Schiel 2004, 2011). However, similar changes from domination of large canopy forming seaweeds to habitats dominated by opportunistic turf algae have occurred throughout the world particularly associated with anthropogenic stressors like eutrophication, warming, sedimentation and invasive species (Eriksson et al. 2002, Connell et al. 2008, Perkol-Finkel and Airoldi 2010, Moy and Christie 2012, Filbee-Dexter et al. 2016, Wernberg et al. 2016). It is also well known that these turfs can inhibit new recruitment of the canopy forming species (Kennelly 1987a, Reed 1990, Dayton et al. 1992, Alestra et al. 2014). Thus, it is possible, that if turfs persist over time, recovery of bull kelp will be impeded from a 'triple-whammy'; (a) propagule pressures will be dramatically lowered because only few *D. poha* and *D. antarctica* have survived on each reef and propagule dispersal may be spatially very limited (Taylor and Schiel 2005, Schiel and Foster 2006), (b) propagule settlement and early survival can be strongly inhibited by the turf alga (Schiel and Foster 2006), and (c) any recruits that survive the two previous bottle necks may be annihilated by fast moving herbivorous fishes (Taylor and Schiel 2010, Bennett et al. 2015, Franco et al. 2017). These inhibition mechanisms could therefore potentially reveal large scale hysteresis effects where recovery may be impeded for long periods of time. Finally, it is possible to speculate on the wider ecological implications of lost bull kelp and possible cascading impacts on other organisms. First, there would clearly have been a massive loss of holdfast-associated invertebrates. Each bull kelp holdfast supports highly diverse communities dominated by crustaceans and gastropods (see Chapter 2, McLay and Hayward 1987, Anderson et al. 1997, Anderson et al. 2005) that now have lost their habitat. Furthermore, several species have adapted to shading and whiplash from bull kelp, such as flat encrusting coralline alga, *Codim dimorphum* and various small understory red and green algae (Taylor and Schiel 2005). These species are typically inferior in competition with turf algae and have been similar severely reduced following the earthquake (pers. obs.). Finally, more complex indirect effect may have occurred such as reduced recruitment of abalone larvae that normally settle on the understory encrusting coralline alga (Troell et al. 2006), as well as other effects on butterfish and other

herbivores that consume bull kelp (Taylor and Schiel 2010, Bennett et al. 2015) or even on adjacent de-compositional beach communities that depend on continuous supply of beach casts seaweed wracks (Malm et al. 2004).

4.5.3 Conclusions

With this work, I showed extensive and severe negative impacts of coastal uplift on bull kelp, outlining a series of responses from loss of blades, to loss of stipes to dislodgment of holdfasts. I suggest that these changes will have long lasting and wide ranging ecological impacts on the plant and animal communities normally associated with bull kelp beds and highlight that it is imperative to follow bull kelp recovery (or lack of) over years and decades to come to better understand the ecology of this particular coastline, and, more generally, how large scale disturbances affect natural communities.

4.6 Tables

Table 4.1 Locations, sampling dates, uplift and number of samples collected from the white (higher), green (middle) and red (lower) elevation zones, three zones that all were dominated by bull kelp prior to the earthquake. Uplift data was extracted from nearest measured location, typically within 1-200 m from the sampled reef (Uplift data courtesy of geologist Kate Clark).

Km from Oaro	Sampling date	Latitude	Longitude	Topography	Uplift (m)	White	Green	Red
0.00	29/03/2017	-42.51594	173.50903	Flat rocks	-0.20	0	8	118
1.35	3/01/2017	-42.50339	173.51281	Boulders	2.18	63	56	42
2.05	3/01/2017	-42.49919	173.51908	Boulders	1.22	51	62	0
3.59	15/02/2017	-42.48714	173.52682	Boulders	1.66	23	58	0
3.80	15/02/2017	-42.48541	173.52760	Boulders	1.66	30	40	0
4.18	17/02/2017	-42.48236	173.52908	Boulders	1.52	32	98	1
4.67	17/02/2017	-42.47764	173.53165	Boulders	1.16	67	66	0
5.40	16/02/2017	-42.47217	173.53695	Boulders	1.02	31	70	2
5.91	16/02/2017	-42.46760	173.53869	Boulders	1.01	44	61	0
6.63	2/03/2017	-42.46259	173.54512	Boulders	0.72	15	51	0
7.14	2/03/2017	-42.45883	173.54866	Flat/Cut	0.36	21	52	32
7.40	2/03/2017	-42.45822	173.55376	Flat/Cut	0.40	20	49	12
17.52	9/03/2017	-42.43351	173.69029	Boulders	0.69	6	96	8
17.54	10/03/2017	-42.43517	173.69176	Flat/Cut	0.91	2	51	10
19.63	30/03/2017	-42.42697	173.71468	Flat/Cut	0.57	3	40	15
19.91	30/03/2017	-42.42528	173.71692	Flat/Cut	0.57	4	89	59

Table 4.2 Mann-Whitey test results comparing bull kelp responses from uplifted reefs vs. Oaro for the green (middle elevation) and red (lower elevation) elevation zone. See figure 4.1 for graphical results (grey vs. white bars). The white zone data were excluded because this zone was absent from Oaro.

Bull kelp response	**Stat.**	**Green**	**Red**
Scars (%)	Z	-1.527	-2.682
	p	0.127	**0.007**
Scars (#)	Z	-1.591	-2.635
	p	0.111	**0.008**
Stipe without blades (#)	Z	-3.206	-7.501
	p	**0.001**	**0.000**
Stipe with blades (#)	Z	-1.370	-0.669
	p	0.171	0.504
Holdfasts (%)	Z	-2.218	-4.434
	p	**0.027**	**0.000**

Table 4.3 Mann-Whitey test results comparing bull kelp responses between elevation zones (white = higher, green = middle, red = lower). See figure 4.1 for graphical results (grey bars only). Oaro responses were excluded from this analysis.

Bull kelp response	**Stat.**	**Red vs. Green**	**Red vs. White**	**Green vs. White**
Scars (%)	Z	-3.719	-8.980	-9.549
	p	**0.000**	**0.000**	**0.000**
Scars (#)	Z	-3.999	-9.556	-10.172
	p	**0.000**	**0.000**	**0.000**
Stipe without blades (#)	Z	-6.218	-0.661	-7.547
	p	**0.000**	0.509	**0.000**
Stipe with blades (#)	Z	-22.517	-18.401	-1.881
	p	**0.000**	**0.000**	0.060
Holdfasts (%)	Z	-5.558	-10.776	-8.278
	p	**0.000**	**0.000**	**0.000**

Table 4.4 Spearman rank correlation analysis between five bull kelp responses and degree of uplift. Se figure 4.3-4.7 for corresponding graphical analysis. Significant results are highlighted in bold.

Bull kelp response	**Stat.**	**White**	**Green**	**Red**
Scars (%)	r	0.055	0.121	-0.343
	p	0.859	0.681	0.366
Scars (#)	r	0.412	0.297	0.067
	p	0.162	0.303	0.864
Stipe without blades (#)	r	0.204	0.121	0.417
	p	0.505	0.681	0.265
Stipe with blades (#)	r	-0.355	-0.758	0.300
	p	0.233	**0.002**	0.433
Holdfasts (%)	r	0.049	0.244	0.633
	p	0.873	0.401	0.067

Figure 4.1 Photos. A = healthy reef without uplift, B = white zone seen from the shore, C = aerial shore landscape: white, green and red zone as seen from above. D = white zone. E = decaying process on a holdfast plant, F = green zone seen from the shore, G = typical green zone with quadrat used for the surveys. H = *Ulva* colonized the space left by bull kelp, I = red zone. Quadrate size on photos is 0.5 × 0.5 m.

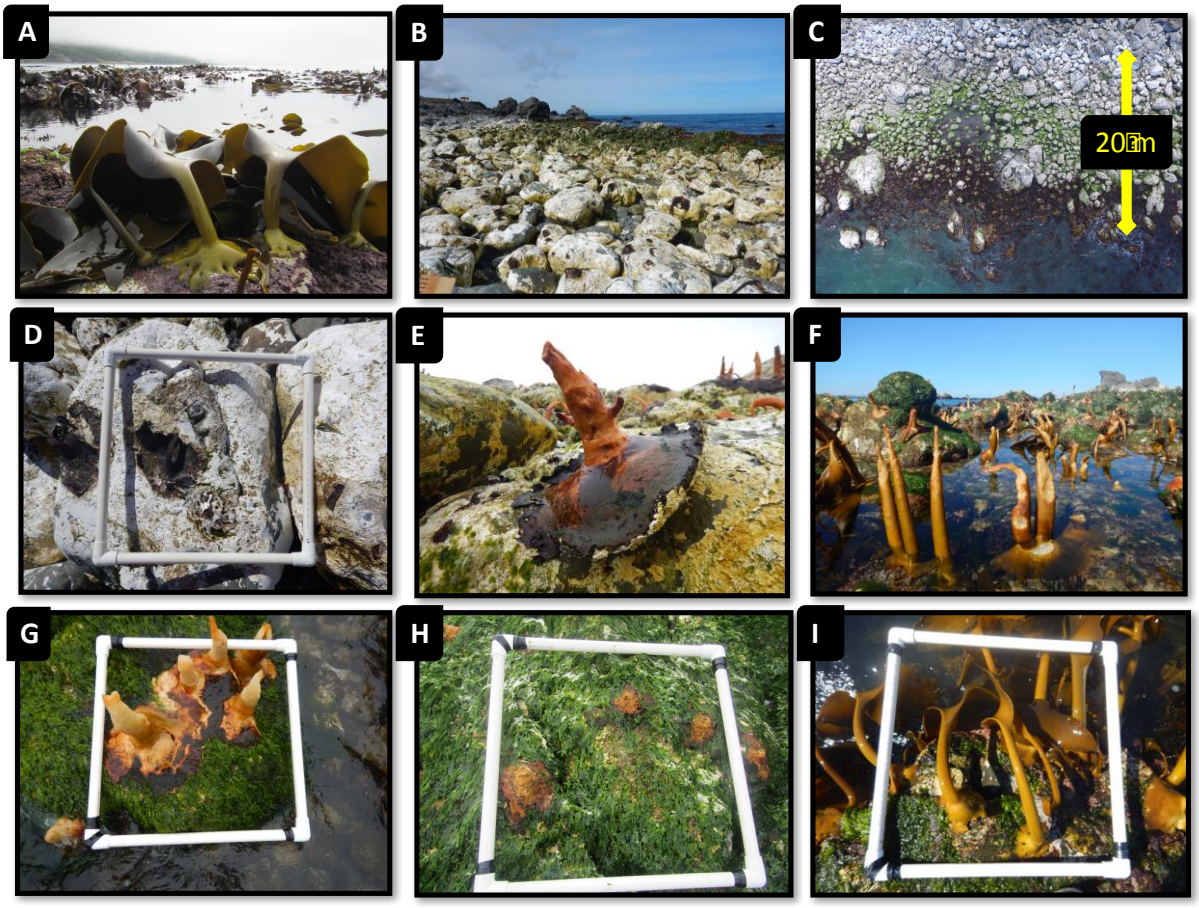


Figure 4.2 Percent cover of holdfast scars (A), density of holdfast scars (B), density of stipes without blades (C), density of stipe with blades (D) and, percent cover of holdfasts (E) for the white, green and red elevation zones. Data are presented per 0.25 m^2 quadrat, error bars are SE, n from left = 0, 412, 8, 939, 118, 181. X axis legend; NW = no uplifted white zone, UW = uplifted white zone, NG = no uplifted green zone, UR = uplifted red zone, NR = no uplifted red zone, UR = uplifted red zone. Note that there were no 'white' zone with bleached calcified encrusting organisms and kelp scars at Oaro (NA). See Table 4.1 for details about reefs.

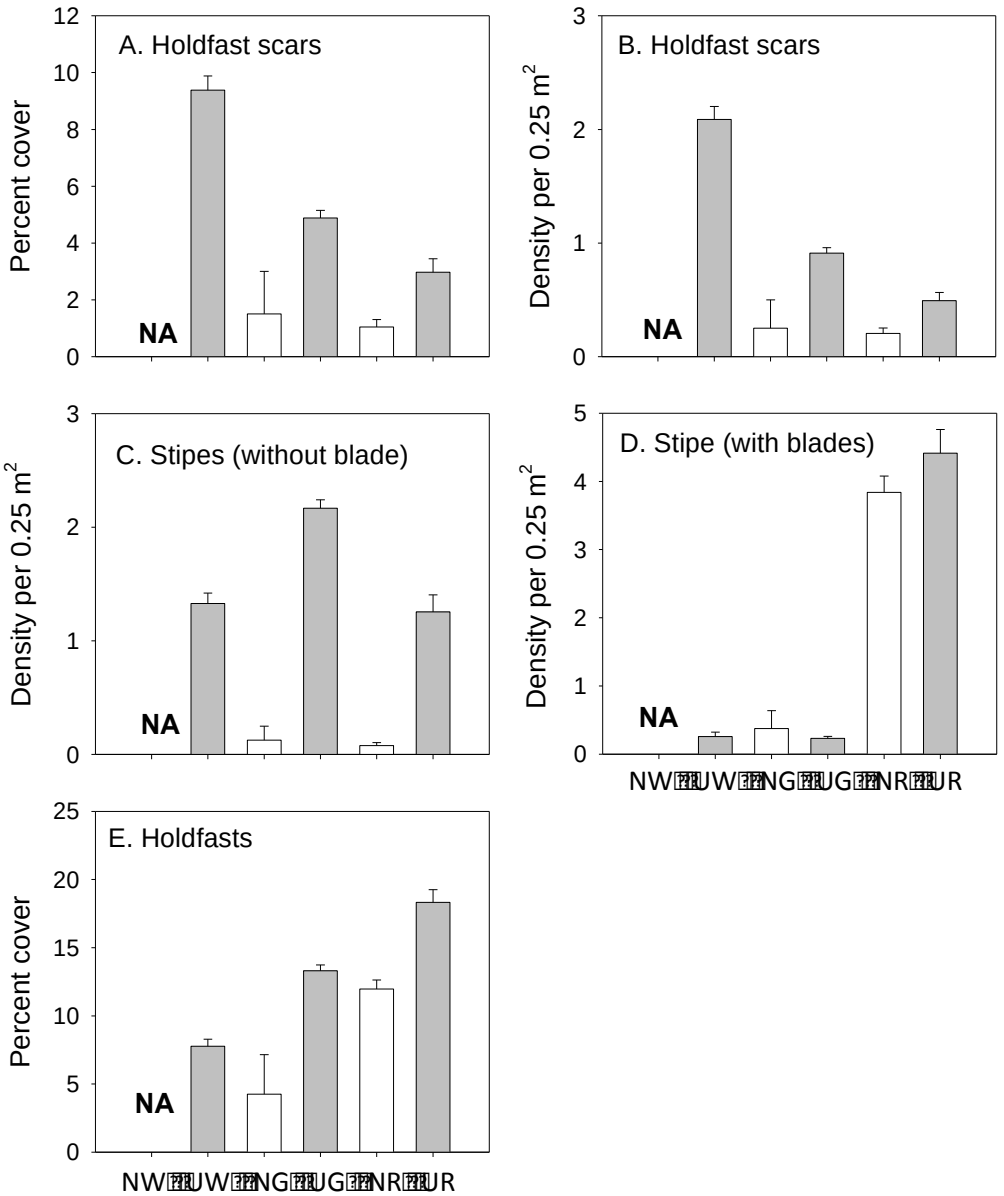


Figure 4.3 Percent cover of holdfast scars plotted against intensity of uplift (m) for the white zone (A), green zone (B) and red zone (C). Note that one reef (Oaro) experienced 20 cm submergence (and this reef had no white zone). See table 4.1 and figure 4.1 for details about sample reefs, zones and sample sizes.

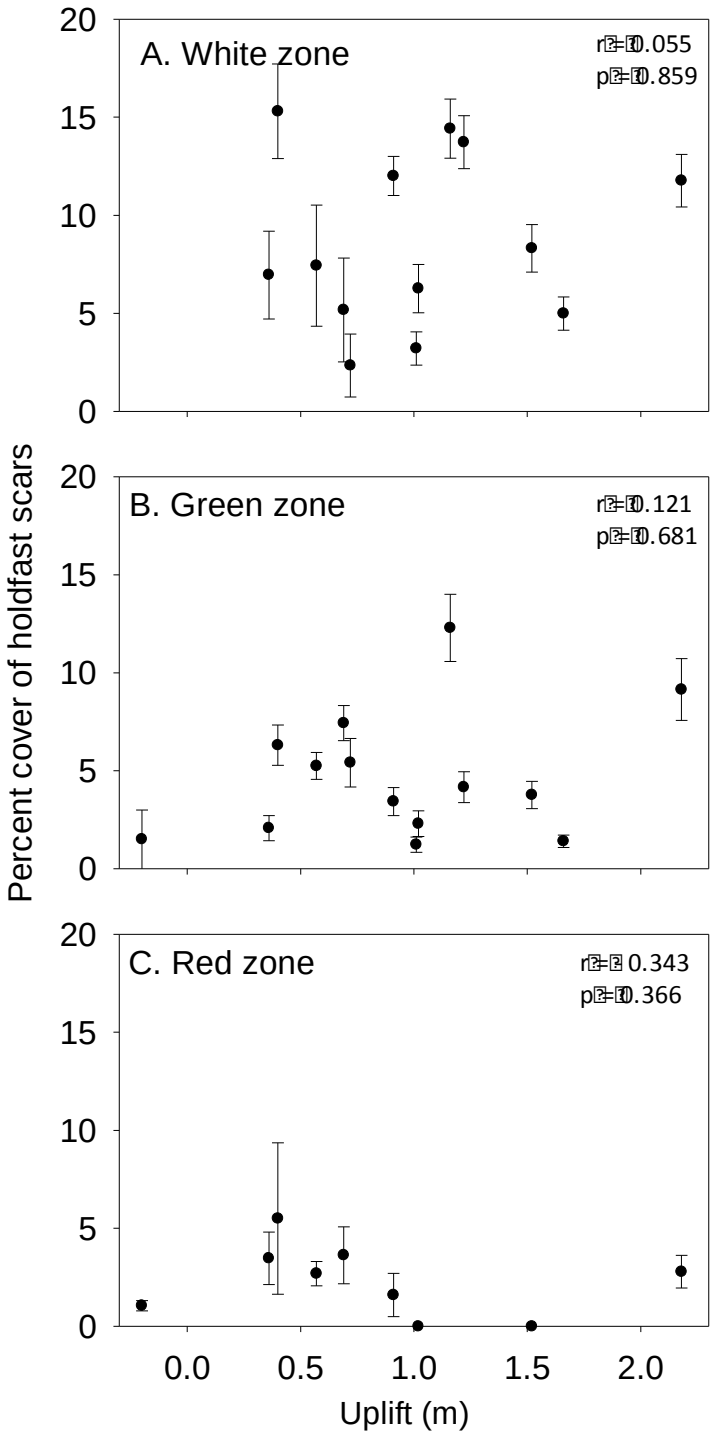


Figure 4.4 Density of scars plotted against intensity of uplift (m) for the white zone (A), green zone (B) and red zone (C). Note that one reef (Oaro) experienced 20 cm submergence (and this reef had no white zone). See table 4.1 and figure 4.1 for details about sample reefs, zones and sample sizes.

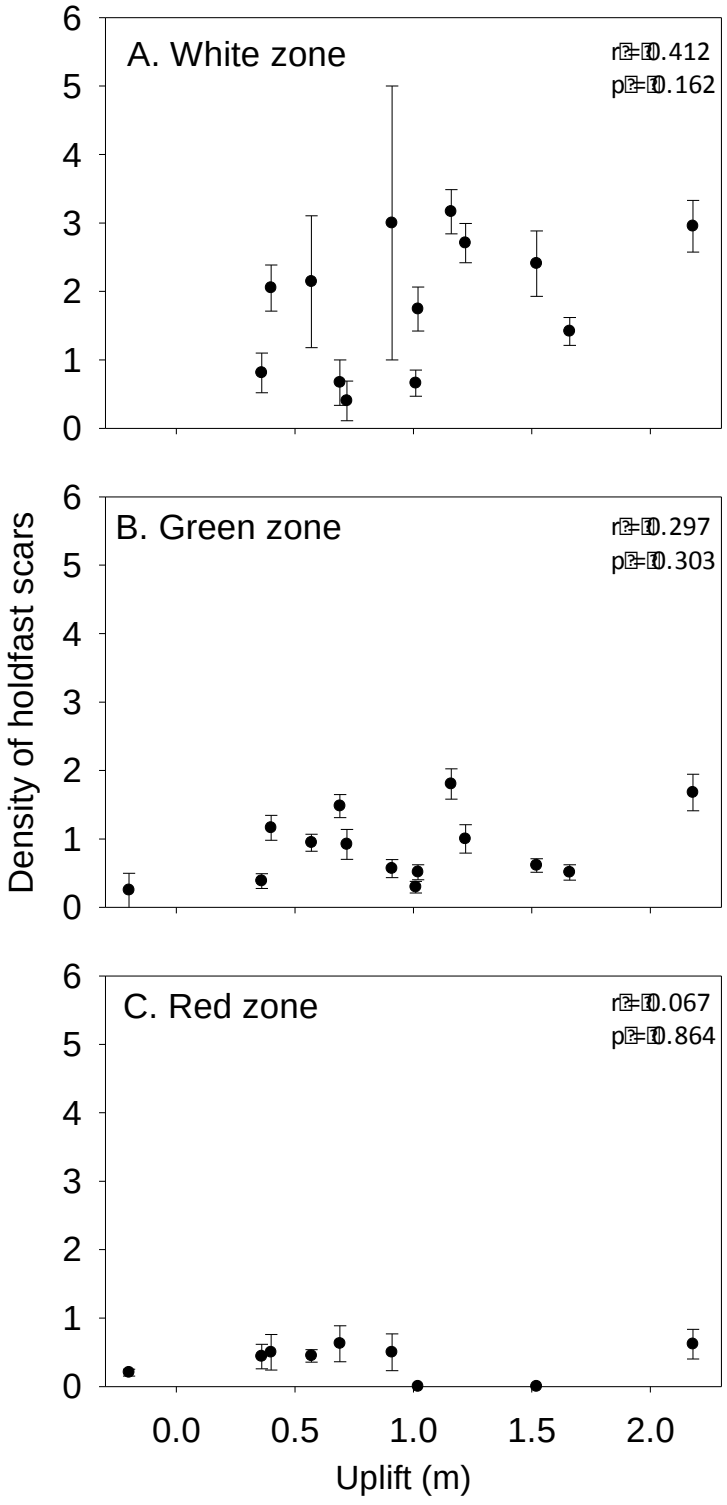


Figure 4.5 Density of stipes without blades plotted against intensity of uplift (m) for the white zone (A), green zone (B) and red zone (C). Note that one reef (Oaro) experienced 20 cm submergence (and this reef had no white zone). See table 4.1 and figure 4.1 for details about sample reefs, zones and sample sizes.

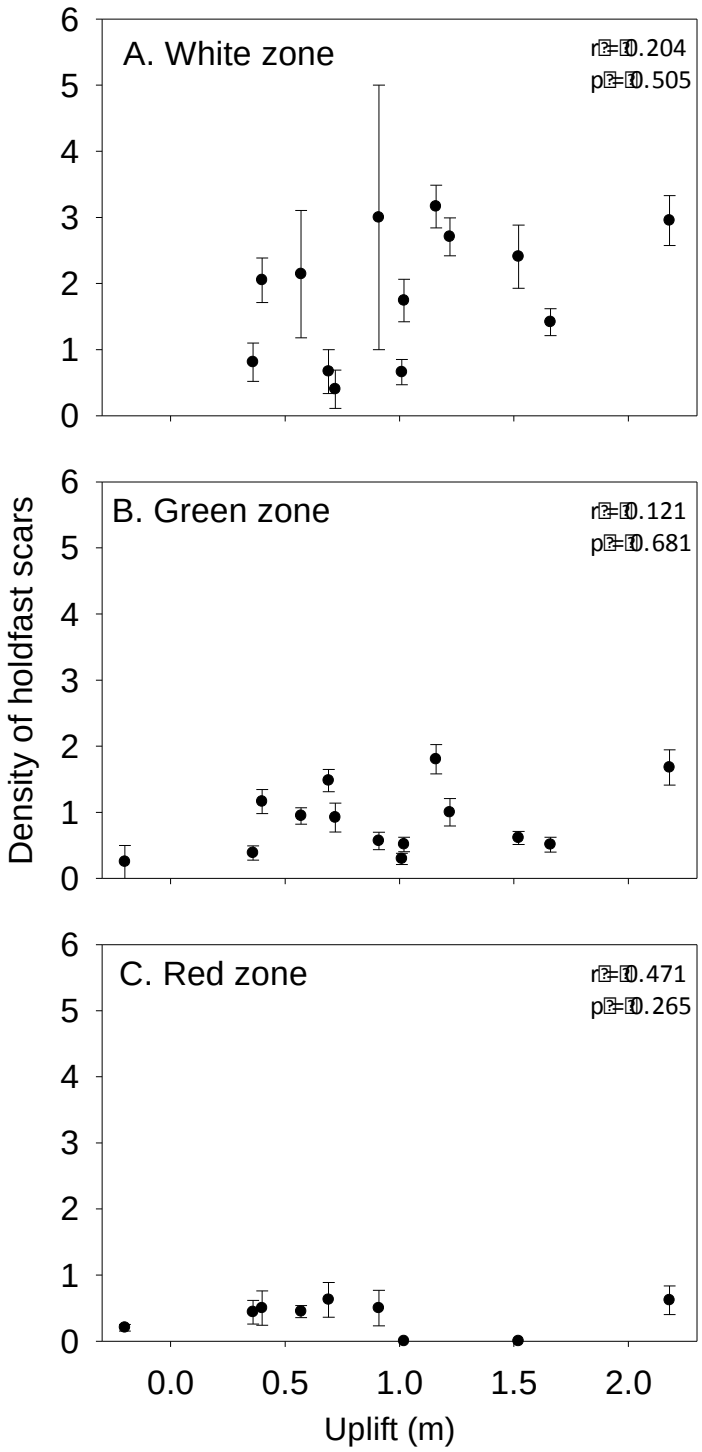


Figure 4.6 Density of stipes with blades plotted against intensity of uplift (m) for the white zone (A), green zone (B) and red zone (C). Note that one reef (Oaro) experienced 20 cm submergence (and this reef had no white zone). See table 4.1 and figure 4.1 for details about sample reefs, zones and sample sizes.

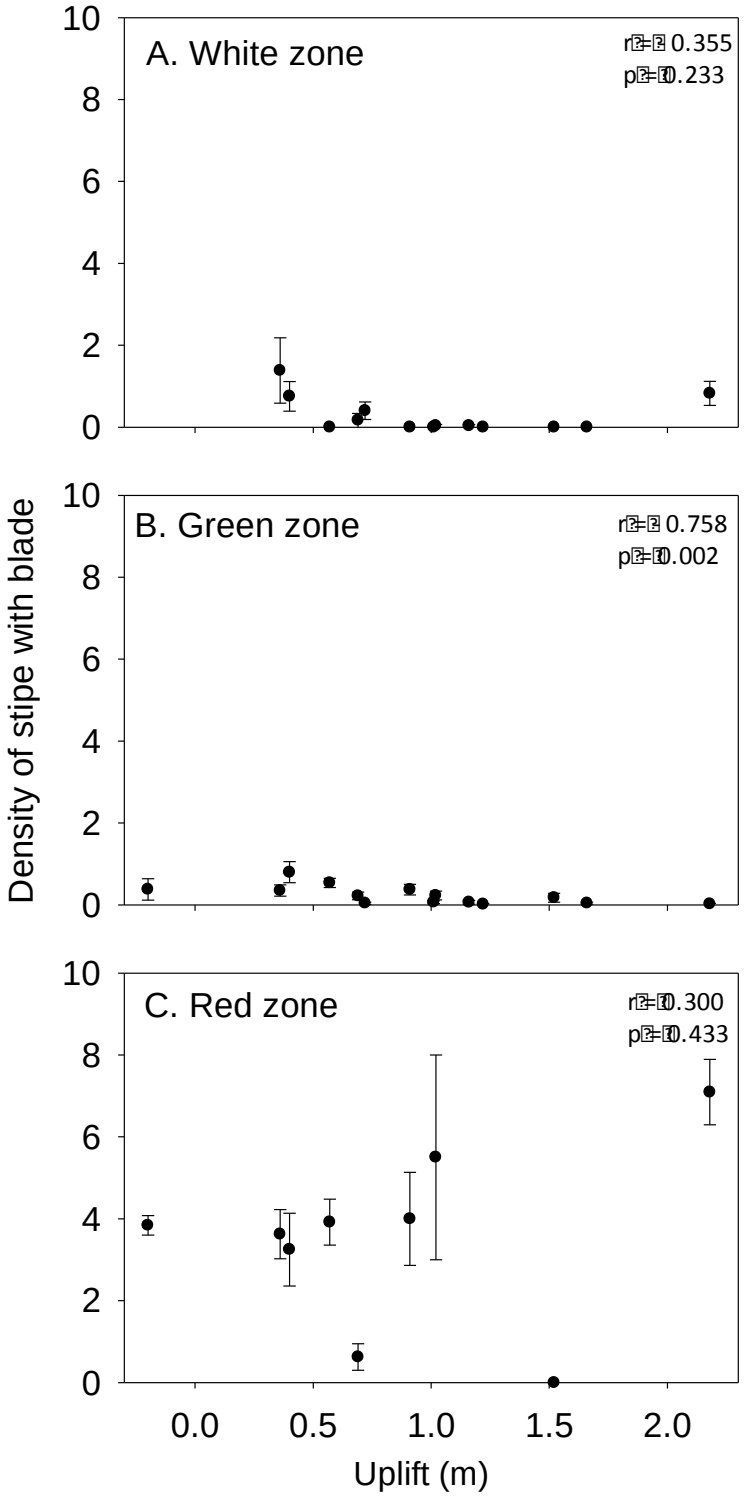
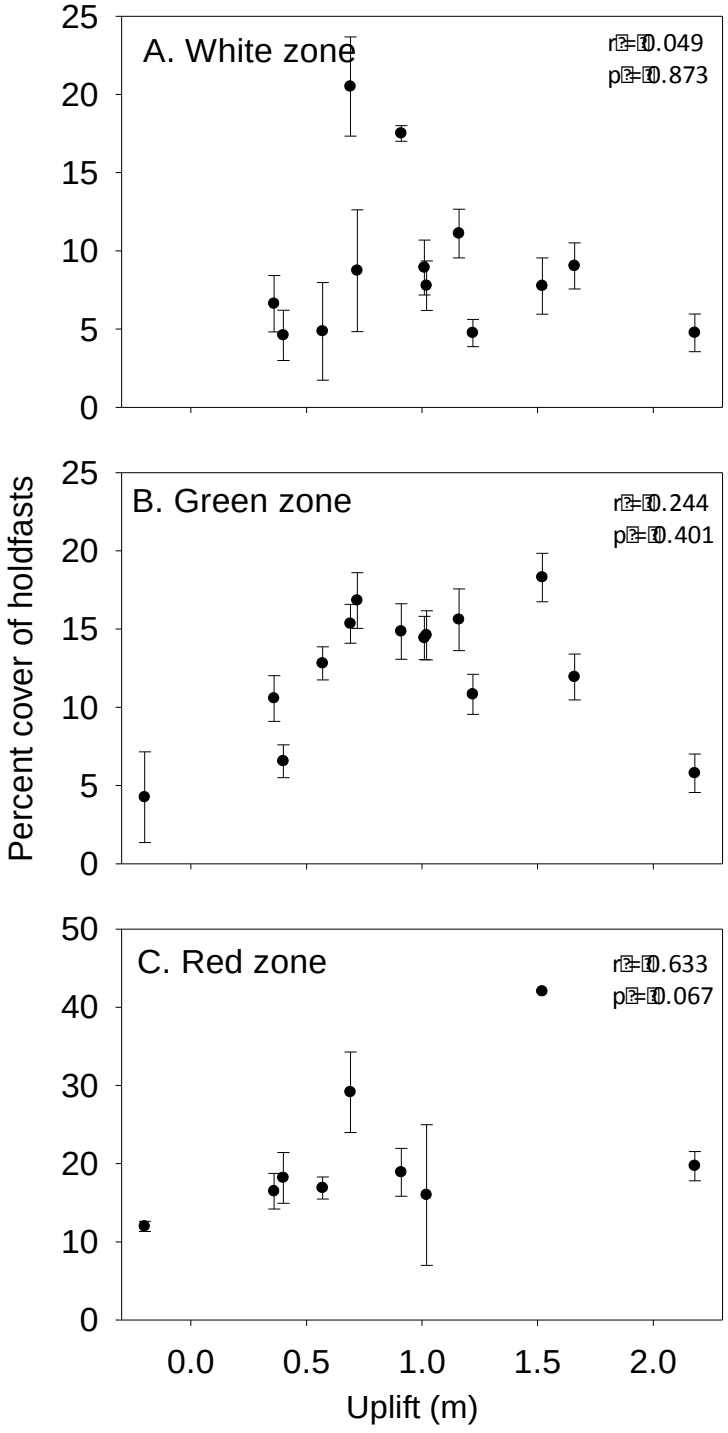


Figure 4.7 Percent cover of holdfasts plotted against intensity of uplift (m) for the white zone (A), green zone (B) and red zone (C). Note that one reef (Oaro) experienced 20 cm submergence (and this reef had no white zone). See table 4.1 and figure 4.1 for details about sample reefs, zones and sample sizes.



Chapter 5: Discussion

5.1 Background

Kelp forests and fucoid beds are highly productive marine habitats that increase biodiversity (Steneck et al. 2002, Schiel and Foster 2015). These brown macroalgae increase productivity, attenuate waves, provide food for grazers and habitat for benthic organisms, and are therefore commonly referred to as 'foundation species' (Cancino and Santelices 1980, Smith and Bayliss-Smith 1998, Bruno and Bertness 2001, Stachowicz 2001, Edgar et al. 2004, Taylor and Schiel 2010, Teagle et al. 2017). In New Zealand, bull kelp species, like *Durvillaea antarctica* and *D. poha,* often dominate intertidal rocky shores (Hay 1977, Schiel and Hickford 2001, Fraser et al. 2012, Schiel et al. 2016). However, the harsh environment of this zone also exposes bull kelp to an array of stressors and disturbances, such as storm waves, grazing, competition with opportunistic species, harvesting, sediment pollution, etc. (Ebeling et al. 1985, Kennelly 1987a, Bustamante and Castilla 1990, Wernberg and Connell 2008, Taylor and Schiel 2010). In particular, long-lived holdfasts of bull kelp are of ecological importance as they provide a specialised habitat for many benthic invertebrates (Cancino and Santelices 1980, Ojeda and Santelices 1984, Edgar et al. 2004). Ecological data on bull kelp, their holdfasts and how they respond to disturbances are therefore highly relevant for the conservation and management of temperate wave exposed rocky intertidal marine environments of the southern hemisphere.

5.2 Disturbance and its effects on bull kelp

Many studies have documented the effects of disturbance on stands of kelps and fucoids, typically quantifying effects related to natural disturbances such as grazing (Taylor and Schiel 2010), physical disturbance such as storms (Ebeling et al. 1985, Seymour et al. 1989, Lilley and Schiel 2006, Schiel et al. 2006, Schiel et al. 2018) or from anthropogenic stressors, such as eutrophication and climate change (Bustamante and Castilla 1990, Estes and Duggins 1995, Graham 2004, Connell and Russell 2010, Schiel et al. 2016, Wernberg et al. 2016). Many of these studies have shown that kelps and fucoids can recover from small scale disturbances, often from growth of sub-canopy juveniles, but this process can take many years (Kennelly 1987b, Schiel and Taylor 1999, Taylor and Schiel 2005, Wernberg 2006, Schiel and Lilley 2011, Tait and Schiel 2011b). I found that although bull kelp densities were highly variable among sites and disturbance treatments, juvenile bull kelp could grow fast over just a few months, supporting the findings of earlier studies (Hay 1977, Taylor and Schiel 2005). Variable densities of understory juvenile kelps and fucoids have been documented in many studies, for

example varying between years, sites, season of disturbances (Taylor and Schiel 2005) and temperatures, where cold and warm conditions can either facilitate or inhibit juvenile growth following canopy removals (Wernberg et al. 2010). I also found that when entire blades were removed (by cutting stipes), bull kelp did not recover. Westermeier et al. (1994) and Hay (1977) initially reported survival from stipe cutting. However, over a longer period, the cut stipes and holdfast eventually degraded and the individuals died. By contrast, when adult blades were pruned (i.e., removed above the stipe-blade meristem) individuals showed sign of new growth, thereby suggesting that bull kelp have two recovery mechanisms depending on the severity of disturbance event (Chapter 2, i.e., either through regrowth of blades or new grow of juveniles). Finally, I found no decreases in holdfast size or holdfasts density four months after disturbances, reflecting that the decay of bull kelp holdfasts is slow, as shown before (Hay 1977, Westermeier et al. 1994, Taylor and Schiel 2005).

In addition to small scale disturbances, entire reefs and regions can be disturbed, for example when urchins convert beds of canopy-forming seaweed to 'barrens' (Breen and Mann 1976, Mann 1977, Chapman 1981, Scheibling et al. 1999), when invasive species outcompete kelp (Levin et al. 2002) or following unusually warm conditions (Wernberg et al. 2010, Johnson et al. 2011, Wernberg et al. 2016). However, even for such large scale disturbance events, recovery is potentially possible if grazers and invaders are removed and waters get colder (but perhaps unlikely, particularly for warming stress). By contrast, few studies have reported large scale die-off of kelps and fucoids from disturbances where recovery is unlikely, for example following earthquake related uplift events (Castilla et al. 2010). During such events, entire intertidal communities are moved upwards relative to sea-level exposing them to increased levels of desiccation stress, a stressor that often limits dominant canopy forming seaweed and have cascading ecological impacts (Stephenson and Stephenson 1949, Kensler 1967). In this context, the 7.8 M_w Kaikōura earthquake of November 14th, 2016 represented a rare opportunity to assess the impact of a massive physical disturbance, by comparing ecological differences between small (experimental) and large (uplift)-scale disturbance events. Following the earthquake, reefs along the coastline from Oaro to Kaikōura were uplifted from 0.4 to 2.2 m (Chapter 4), a region-wide disturbance to intertidal communities, and a type of reef-wide disturbance that mainly has been studied in Chile and Japan (Castilla 1988, Castilla and Oliva 1990, Castilla et al. 2010) Horiguchi et al. 2016). Three months after the Kaikōura earthquake, I quantified extensive mortality of bull kelp at 15 uplifted reefs, with most severe impact in the upper part of the bull-kelp zone (a zone that turned 'white' from dying encrusting

algae), medium impact, just below this level (a zone that turned 'green' from colonizing turf-forming *Ulva* species), and the least impact in a lower zone (termed the "red-zone" because the red encrusting understory algae survived here (this zone was still dominated by *Durvillaea willana*) (Chapter 4). In the 'red' zone most of bull kelp holdfasts remained attached to the substratum and appeared healthy with large blades still attached, and the sub-canopy species were still dominated by the red encrusting algae (see Chapter 4, Taylor and Schiel 2005, Schiel et al. 2018). Above this zone, either blade sizes were strongly reduced, blades were lost entirely, stipes (with blades) were lost, or entire holdfasts were dislodged (leaving 'holdfasts scars'; note that I could not identify the specific *Durvillaea* species because of the missing blades). Similar different levels of dieback have been described from both natural and manipulated disturbances to bull kelp (Hay 1977, Westermeier et al. 1994) and was confirmed in my disturbance experiment (Chapter 2). Differences between blade recovery in the manipulative experiment in Chapter 2, and recovery in the green and white zones following reef uplift, reflect that the experiment was done on an un-impacted reef, in contrast to the uplifted reefs where bull kelp habitats were converted to permanently dryer environments (Castilla 1988, Castilla and Oliva 1990, Castilla et al. 2010). Indeed, the impacts reported on bull kelp from the Kaikōura uplift were very similar to permanent impacts on intertidal *D. antarctica* and *Lessonia nigrescens* following the March 3rd, 1985 uplift along the Chilean coastline (Castilla 1988, Castilla and Oliva 1990, Castilla et al. 2010). After this earthquake, the blades of these seaweed species were lost first, followed by colour changes to holdfasts and eventually, over one year, detachment from the substratum. Still, what I have observed in my survey (Chapter 4) and experiment (Chapter 2) suggests that damaged bull kelp holdfasts persist long after being severely disturbed, for example allowing associated invertebrates time to colonize other habitats (discussed later).

5.3 Disturbances to bull kelp; effects on opportunistic algae

When blades from large seaweeds are lost, so are blade whiplash effects, a process that can control many ecosystem functions and biological community structure (Santelices and Ojeda 1984, Taylor and Schiel 2005, Wernberg et al. 2005, Schiel et al. 2018). In this study, the loss of bull kelp in the experimentally disturbed small-scale plots (Chapter 2) and on the uplifted reef sections (Chapter 4) had a positive effect on the cover of opportunistic seaweed. Four months after the earthquake, much of the uplifted reefs that previously was dominated by blades, holdfasts and juveniles of *D. poha* and *D. antarctica* and an understory of red encrusting

alga, was now colonized by turf forming fast growing *Ulva* species. Similar rapid colonization of small opportunistic species have been described from both New Zealand (Schiel 2004, Schiel and Lilley 2011) and around the world, were blades from kelps and fucoids have either been lost or removed experimentally (Eriksson et al. 2002, Connell et al. 2008, Perkol-Finkel and Airoldi 2010, Moy and Christie 2012, South et al. 2016, Wernberg et al. 2016), highlighting that this is a general ecological process. When these turf forming algae colonize disturbed areas, they may inhibit new kelp recruits through a variety of mechanisms; for example by occupying all available space, chemical allelopatric interactions, shading, competition for nutrients, by providing a weak substratum so that even if kelp attach to turf they will dislodge when exposed to hydrodynamic forces, or by trapping sediments that prevent recruitment (Kennelly 1987a, Reed 1990, Dayton et al. 1992, Schiel et al. 2006, Alestra et al. 2014). It is therefore possible that future bull kelp recovery will be impeded by these turf algae (Kennelly 1987a, Dayton et al. 1992, Schiel et al. 2018). Potential inhibition from turf forming algae was supported by a negative correlation between bull kelp recruits and cover of the opportunistic seaweed *Ulva* (Chapter 2; but alternatively turfs are 'passengers' and kelp recruits 'drivers' of this relationship (South and Thomsen 2016)). Furthermore, it is a long standing paradigm in invasion biology that opportunistic (invasive) species generally are adapted to colonize disturbed habitats (Hobbs and Huenneke 1992, Mack and D'Antonio 1998, Lake and Leishman 2004). I found support for this paradigm because the non-native annual Asian kelp *Undaria pinnatifida* invaded virtually all disturbed plots at the two Moeraki reefs. This invasion, however, was not surprising, as *Undaria* has previously have been shown to invade plots and reefs where canopy-forming seaweed have been disturbed (Valentine and Johnson 2003, 2004, Schiel and Thompson 2012, Thompson and Schiel 2012, South and Thomsen 2016, South et al. 2017, Schiel et al. 2018). In contrast to some turf algal species that in some cases can persist year-round, *Undaria* is seasonal and only dominates on reefs for 5-7 months of the year (Schiel and Thompson 2012, Thompson and Schiel 2012, South and Thomsen 2016, South et al. 2017, Schiel et al. 2018). These differences in seasonal dominance imply that bull kelp perhaps is more likely to recover on reefs where *Undaria,* rather than turf alga, invade.

5.4 Bull fast holdfasts invertebrate communities

Loss of bull kelp is likely to result in many direct and indirect effects on biological communities and ecosystem functions (Smith and Bayliss-Smith 1998, Tait and Schiel 2010, Taylor and Schiel 2010, Tait and Schiel 2011b, a, 2013, Schiel et al. 2018). For example, loss of bull kelp

holdfasts could have great ecological importance, because large seaweed holdfasts typically provide an abundant, but specialised habitat for many invertebrate species (Cancino and Santelices 1980, Sheppard et al. 1980, Ojeda and Santelices 1984, McLay and Hayward 1987, Smith and Simpson 1995, Anderson et al. 1997, Smith and Bayliss-Smith 1998, Thiel and Vásquez 2000, Anderson et al. 2005, Taylor and Schiel 2005, Hauser et al. 2006, Blight and Thompson 2008). More specifically, 23 macroinvertebrate taxa were found associated with intertidal *D antarctica* holdfasts collected from the subantarctic Heard Island (Edgar and Burton 2000), and bull kelp holdfasts from New Zealand CAN provide important habitat for the intertidal spider *Desis marina* (McLay and Hayward 1987) and the trochid snail *Diloma philippi* (Spencer et al. 2009). Interestingly, Edgar et al. (2004) also demonstrated experimentally that many epifaunal invertebrates rapidly abandon detached holdfasts, suggesting that at least some of these species have adapted to a habitat that can dislodge during storms. Still, studies on bull kelp holdfasts fauna are few, only include few collected holdfasts, and target only a few specialist species. Given the high abundance of bull kelp along large stretches of coastlines in the Southern Hemisphere it is important to know more about these invertebrate communities to better understand the effects of bull kelp losses. My holdfast collections and transplant experiment showed that most invertebrates were molluscs and crustaceans, as shown for other holdfast studies (Hauser et al. 2006, Tuya et al. 2011). Furthermore, I found a positive relationship between holdfast size, population density and taxonomic richness of invertebrates, a finding supported in other studies (Cancino and Santelices 1980, Sheppard et al. 1980, Smith 1996, Christie et al. 2003, Anderson et al. 2005, Hauser et al. 2006, Tuya et al. 2011). Such size-abundance relationships could, if coupled with holdfast density and size data (see Chapters 2 and 4), provide a quantitative understanding of the amount of invertebrates lost following disturbances, or of the amount of invertebrates that have to move to other suitable habitats or will become part of the holdfast drift community (Collins et al. 2010, Fraser et al. 2011, Haye et al. 2012, Cumming et al. 2014, Gutow et al. 2015). My results also support the notion that these holdfasts are 'micro-islands' of high biodiversity (Thiel and Vásquez 2000), where invertebrates are buffered from environmental stressors like wave action, desiccation and predation. Furthermore, the persistent holdfasts that can survive for many months after damage to the kelp blade and growth meristem (see Chapter 2, 3, Santelices et al. 1980, Castilla 1988, Castilla and Oliva 1990) may provide an important temporal buffer that allows invertebrates ample time to colonise nearby holdfast before detachment.

Bull kelp holdfasts not only differ in sizes (Chapters 2-4), but also in shape, typically being circular or elongated but sometimes also having complex convoluted shapes (some of the more complex shapes may be caused by multiple holdfasts coalescing) (Hay 1977). I therefore tested whether different holdfast-shapes supported different invertebrate communities with a transplant experiment. Round and elongated shapes generally had the same taxonomic richness and number of invertebrate inhabitants, a finding that was consistent for live holdfasts, holdfast-mimics and also for holdfasts of *Undaria*. This finding thereby does not support larger-scale landscape studies that often find variations among taxa in their preference for different habitat shapes (Cumming 2002, Bull et al. 2006, Riddle et al. 2008). However, there were generally more invertebrates associated with *Undaria* than *Durvillaea* (for similar sized holdfasts) and for live holdfasts compared to mimics (Chapter 3). The most likely reasons for these effects are that *Undaria* and live holdfasts are morphologically more complex than *Durvillaea* and mimic holdfasts; the former having more and finer-scale physical structures, such as intertwined mm-thick haptera that form interstitial spaces of various sizes (Hauser et al. 2006, Tuya et al. 2011). It is also possible that live holdfasts support more invertebrates than mimics because live holdfast not only provide shelter from abiotic stressors and predation, but also a food source for grazers, as shown in other studies (Bologna and Heck 1999, Koivisto and Westerbom 2010, Macreadie et al. 2014). Finally, it is important to point out that *Undaria* holdfasts have an annual life cycle (Hay and Villouta 1993, Schiel and Thompson 2012, South and Thomsen 2016) and only grow to a fraction of the size of mature *Durvillaea* holdfasts (Teagle et al. 2017). Hence, on longer and larger spatio-temporal scales, *Durvillaea* holdfasts represent much larger and more stable habitat, and are therefore likely to support higher biodiversity than the invasive kelp.

5.5 Final conclusions

In conclusion, I showed that intertidal bull kelp provides a crucial habitat for a diverse benthic invertebrate community in its holdfasts. However, these habitats are often subjected to disturbances that can either potentially kill these animals, or require them to find new holdfasts or other habitats. I also documented widespread loss of *Durvillaea* following earthquake related reef uplift, where *Durvillaea* first lost blades, then stipes and finally holdfasts dislodged. I showed that, in contrast to *Durvillaea* from the uplifted reefs, *Durvillaea* affected by more typical physical disturbances (e.g., following storms) can recover either by regeneration of pruned blades or rapid growth of juveniles. Although my experiments showed that responses

to disturbances after only a few months, a full recovery of assemblages typically is a much slower process. Furthermore, both the small scale plots where I removed holdfasts and large scale reefs with vertical uplift were colonized by fast-growing opportunistic seaweed like *Ulva* and *Undaria*, species that potentially may inhibit recovery of *Durvillaea*. I finally suggest that, because *Durvillaea* is a typical foundation species with large and long-lived blades, stipes and holdfasts, these changes are likely to have wide-ranging effect on the general ecology along the Kaikōura coastline. It is therefore crucial to follow *Durvillaea* habitats along this coastline on longer time scales to better understand their recovery processes, as well as ensure sustainable management of the many cultural, recreational and commercial benefits that extensive and healthy bull kelp forests provide.

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